Effects of global climate change on an abundant and widely distributed reptile (*Amalosia lesueurii*)

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Certificate of Original Authorship

I, Santiago Cuartas Villa declare that this thesis is submitted in fulfilment of the requirements of the degree of Master in Science (Research) in the School of Life Sciences, Faculty of Science, at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualification at any other academic institution. This research was supported by the Australian Government Research Training Programme.

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Santiago Cuartas Villa

25th November 2019

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Preface

The main body of this thesis consists of four chapters, including two data chapters that are ready to submit. I have therefore formatted each chapter to general guidelines of ecology journals. This has caused some unavoidable repetition in the species description, and background information in some of the chapters.

At the beginning of each chapter, I have acknowledged all authors involved, in the same order as they appear in the manuscripts soon to be submitted. In all of the chapters, I am listed as the first author and was primarily responsible for conceiving, designing and implementing the research and writing the manuscripts.

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Abstract

Reptiles are susceptible to changes in climate because their physiology and behaviour is strongly influenced by temperature. However, reptiles may adapt to shifts in climate migrating to new areas or altering their nesting behaviour in ways that buffer embryos from thermal stress. In this thesis, I investigated geographic variation in nest site selection in the velvet gecko (*Amalosia lesueurii*), a widely distributed and abundant lizard species. To assess how this species might shift its geographic range in future, I modelled the species current and future distribution using the algorithm MaxEnt.

To examine plasticity in species' nest-site selection, I compared the thermal regimes, physical structure and incident light variables of nests in two geographically distant populations (Morton National Park and Yengo National Park). I found strong positive correlations between air temperatures and nest temperatures, with temperatures in some nests exceeding the species' critical thermal maximum during summer heatwaves. Both populations differed in the physical structure, incident light and thermal characteristics of nest sites, so that mean nest temperatures did not differ between locations. Notably, females from the southern population selected more open nest sites than females from the northern population, suggesting that females can adjust nest-site choice to suit local environments. However, nests in the northern population experienced much higher daily maximum temperatures than nests from the southern population, which could have negative consequences for hatching success during hot summers.

To predict the geckos' future distribution, I used a correlative modelling approach in MaxEnt. Modelling showed that the species has a high predicted occurrence across the Sydney Basin, the New England Tablelands, and the southern part of New South Wales (NSW) North Coast. The most important predictor variable in my models was the mean temperature of the warmest quarter. Potentially, the effects of air temperatures on the embryonic life stage may influence the species distribution. The species is predicted to suffer range contractions under future climatic conditions for every emission scenario. The greatest losses are likely to occur around the Sydney Basin region and New England Tablelands. Loss of the velvet gecko from the Sydney region would have serious consequences for the persistence of the vulnerable broad-headed snake (*Hoplocephalus bungaroides*) which relies on geckos as the main food source. My study gives an insight of the threats and general effects of the rising temperature on an abundant and widely distributed Australian reptile.

Chapter 1. Introduction

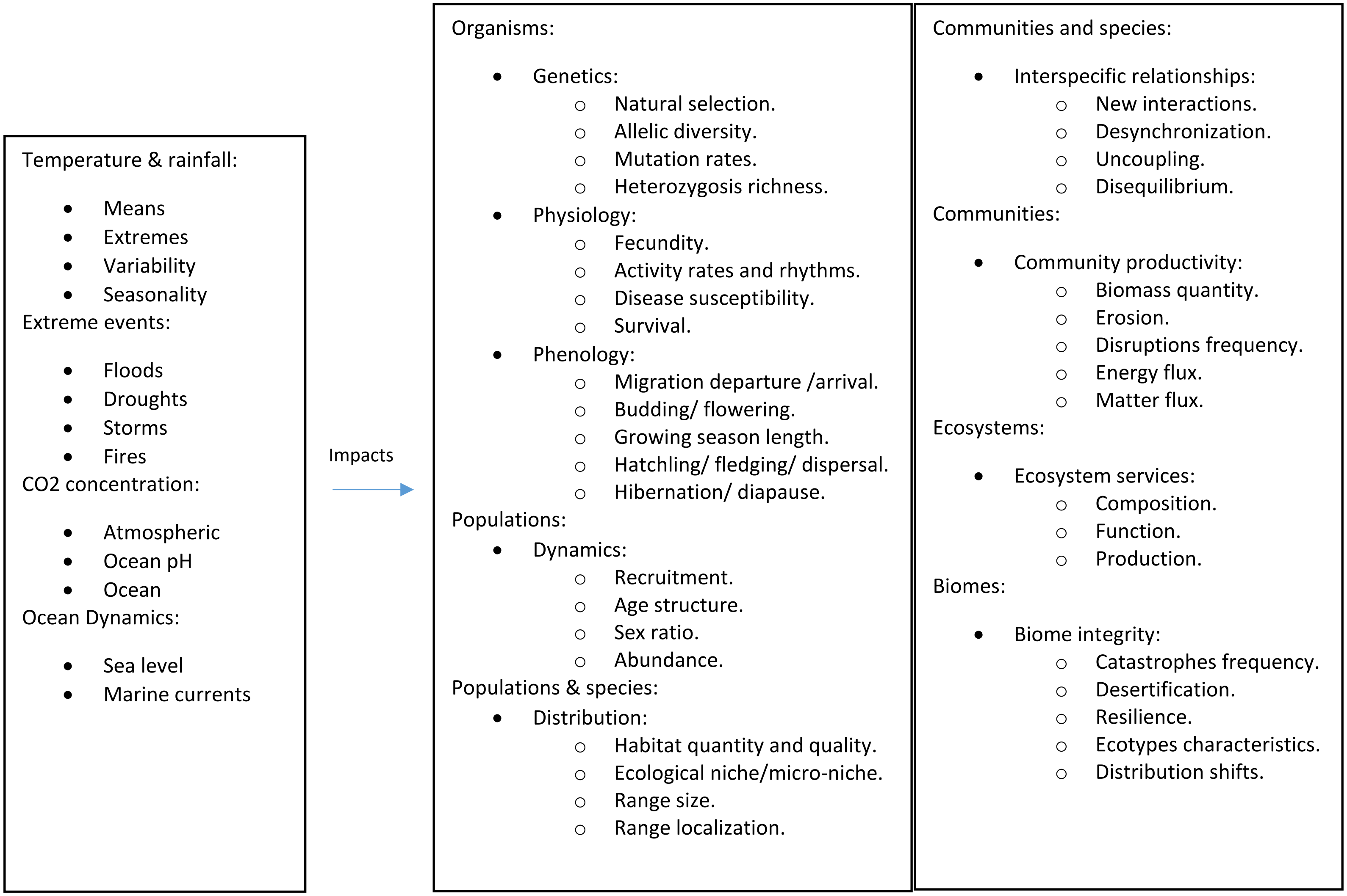
1.1. General threats to biodiversity

The ongoing biodiversity loss from human activities is one of the most catastrophic environmental issues of our time and threatens all ecosystems and also human health that depends on ecosystem services (Ceballos *et al.*, 2015). Between 1970 and 2012 populations of vertebrate species declined by 58% (McRae, Deinet and Freeman, 2017), and 1 million species across all taxa are threatened with extinction (IPBES, 2019). Even conservative estimates of extinction rates for vertebrates exceed by orders of tens and hundreds the historical (natural) average background rates (Dirzo *et al.*, 2014; Ceballos, Ehrlich and Dirzo, 2017). Habitat loss and habitat fragmentation are the major threats for biodiversity (McRae, Deinet and Freeman, 2017). However, pollution and invasive species, and global climate change also pose a great challenge for organisms (IPBES, 2019). Some studies suggest that climate change may be a major driver of biodiversity loss in coming decades (Leadley *et al.*, 2010). In short, we are on the verge of losing the habitats and ecosystems but also the services that biodiversity provides to human welfare (Pecl *et al.*, 2017).

Globally, climates have always changed. Some authors have argued that global mean surface temperatures (GMST) rose over the last century by approximately 0.6 °C (Walther *et al.*, 2002). Temperature increases are natural processes of the interglacial period that the earth is currently going through, and temperatures were higher in the past than those currently witnessed (Zachos *et al.*, 2001). Nonetheless, some researchers have argued that anthropogenic emissions of heat trapping gases have increased the rate of temperature change (Rahmstorf and Coumou, 2011; Coumou and Rahmstorf, 2012; Hansen, Sato and Ruedy, 2012). According to projections under different emission scenarios, modellers predict that GMST will reach 1.5°C above pre-industrial levels if it continues to rise at present rates (IPCC, 2018). While none of the climate models of previous decades have proved accurate, modellers argue that the probability of longer, more severe and more extreme weather events (e.g. heat waves, fires, floods) will increase in future (Coumou and Rahmstorf, 2012; Cowan *et al.*, 2014).

1.2. The effects of climate change on biodiversity

Rising temperatures will affect all levels of biodiversity, ranging from genes, organisms and populations to species, communities and ecosystems (Bellard *et al.*, 2012; Warren *et al.*, 2018, Figure 1). Direct impacts have already been documented all around the globe and on most taxa (Walther *et al.*, 2002; Parmesan, 2006). In order to survive, species will keep adjusting to new environmental conditions either by evolutionary adaptation or phenotypic plasticity (Hendry, Farrugia and Kinnison, 2008; Hoffmann and Sgrò, 2011; Merilä and Hendry, 2014). Species may track suitable microhabitats by migrating or they may adapt to new conditions by altering the timing of reproduction (Parmesan and Yohe, 2003; Parmesan, 2006). Alternatively, species may adapt to new conditions via developmental plasticity (Hendry, Farrugia and Kinnison, 2008; Levy *et al.*, 2016; Telemeco *et al.*, 2017).



Temperature & rainfall:

- Means
- Extremes
- Variability
- Seasonality

Extreme events:

- Floods
- Droughts
- Storms
- Fires

CO2 concentration:

- Atmospheric
- Ocean pH
- Ocean

Ocean Dynamics:

- Sea level
- Marine currents

Organisms:

- Genetics:
    - Natural selection.
    - Allelic diversity.
    - Mutation rates.
    - Heterozygosis richness.
- Physiology:
    - Fecundity.
    - Activity rates and rhythms.
    - Disease susceptibility.
    - Survival.
- Phenology:
    - Migration departure /arrival.
    - Budding/ flowering.
    - Growing season length.
    - Hatchling/ fledging/ dispersal.
    - Hibernation/ diapause.

Populations:

- Dynamics:
    - Recruitment.
    - Age structure.
    - Sex ratio.
    - Abundance.

Populations & species:

- Distribution:
    - Habitat quantity and quality.
    - Ecological niche/micro-niche.
    - Range size.
    - Range localization.

Communities and species:

- Interspecific relationships:
    - New interactions.
    - Desynchronization.
    - Uncoupling.
    - Disequilibrium.

Communities:

- Community productivity:
    - Biomass quantity.
    - Erosion.
    - Disruptions frequency.
    - Energy flux.
    - Matter flux.

Ecosystems:

- Ecosystem services:
    - Composition.
    - Function.
    - Production.

Biomes:

- Biome integrity:
    - Catastrophes frequency.
    - Desertification.
    - Resilience.
    - Ecotypes characteristics.
    - Distribution shifts.

Figure 1. Summary of some of the predicted aspects of climate change and some examples of their likely effects on different levels of biodiversity. Adapted from (Bellard *et al.*, 2012).

Some organisms respond to changing temperatures by tracking optimal niches in higher altitudes or latitudes. Both types of migration have been already documented extensively across many taxa (Sekercioglu *et al.*, 2008; Bellard *et al.*, 2012). Thomas (2010) reviewed range shifts across different taxa, (millipedes; woodlice; spiders; aquatic bugs; butterflies; carabid, long-horn & soldier beetles; dragonflies & damselflies; grasshopper relatives; lacewings; fish; herptiles; birds; mammals), and estimated expansions of range towards the poles in 68% of all species in Britain responding to climate change on the last 30 years. However, these range shifts are in general limited by the dispersal abilities of the organisms (Araújo and New, 2007). While some populations may migrate to novel areas, species with restricted dispersal ability (because of their low vagility or loss of connectivity between habitats due to human activity) may experience local extinctions. Populations that are unable to disperse will experience challenging environmental conditions that could promote extinctions (Figure 2). Recent studies have reported that rises in temperature have already caused widespread local extinctions among plants and animals (see Wiens, 2016, reviewing the topic). One study that modelled the projected geographic ranges under climate change, and which incorporated dispersal limitation, found that 49% of the insects, 44% of plants, and 26% of the vertebrates that were studied (sample sizes of 19,848; 73,224 and 12,429 species respectively) will lose more than 50% of their projected geographic range by 2100 (Warren *et al.*, 2018).

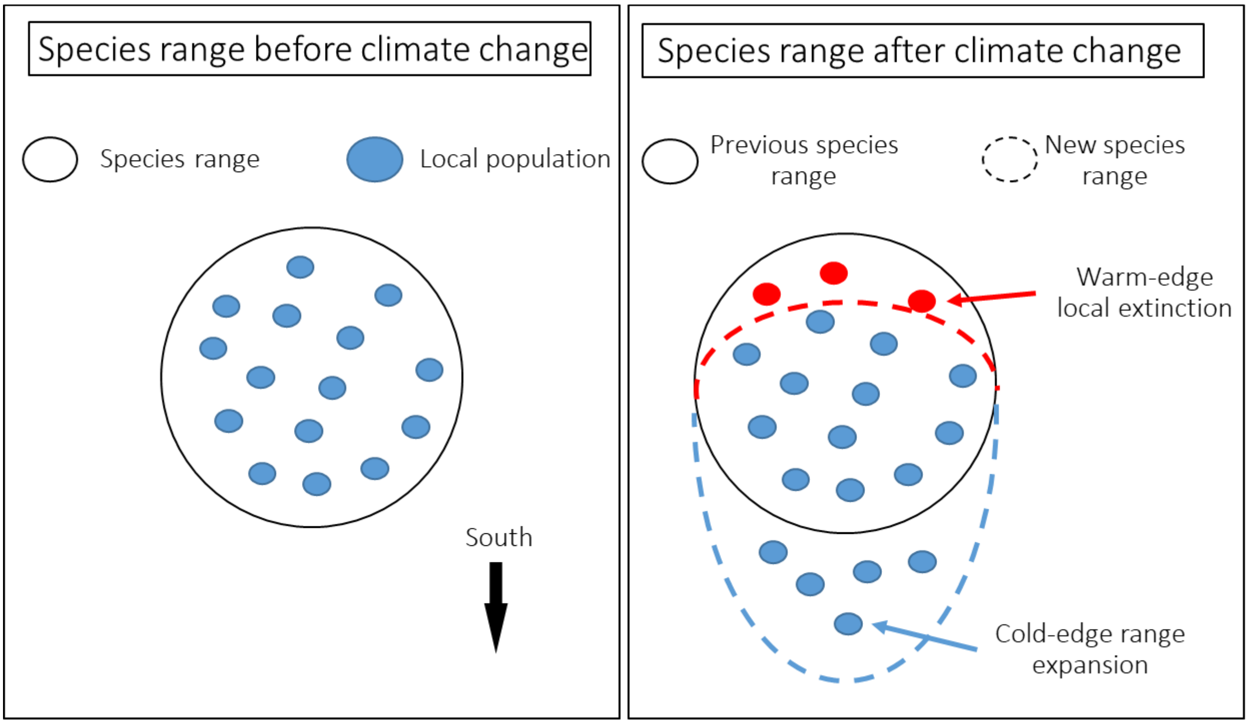


Figure 2. Illustration of geographic range shifts due to climate change on the southern hemisphere (modified from Wiens, 2016).

Range shifts, in conjunction with the increase in global transportation and spread of alien species, may also lead to disrupted communication pathways, novel disease outbreaks or the spread of extant pathogens to new areas. Sarmiento-Ramírez *et al.* (2014) identified two fungal pathogens as potential threats to survival of sea turtle species across the globe. The fungi's optimal growth temperature coincides with the optimal incubation temperature for eggs of many species, and therefore poses a major risk for those species. The study also found environmental temperatures were correlated with the likelihood of disease, thereby increasing turtle species' susceptibility to disease in future. Moreover, recent research reported a decrease in chemical communication for high altitude lizard species with increases in temperature (Iglesias-Carrasco *et al.*, 2018).

Many species alter their phenology in response to weather conditions. Several species of plants and animals have been reported to time their reproduction, blossoming, or migration 5.1 days earlier per decade (on average), with some species breeding up to 24 days earlier in a period of 50 years (Root *et al.*, 2003). Additionally, at smaller scales, some species will adjust to the new environmental conditions by changing their daily activity patterns and behaviours (Sinervo *et al.*, 2010; Levy *et al.*, 2015). In consequence, there may be changes in communities and ecosystems due to decoupling of interspecific relationships like competition, predation, host-parasite interactions, and pollination (Lafferty, 2009; Walther, 2010).

1.3. Effects of the thermal environment on reptiles

The body temperatures of reptiles influence their physiological and behavioural processes (Huey and Stevenson, 1979; Angilletta, 2006). Most reptiles thermoregulate by selecting suitable microhabitats with different environmental temperatures (Arnold, 1983; Ortega, Mencía and Pérez-Mellado, 2016), by changing their colour, and employing different behaviours (Avery, Bedford and Newcombe, 1982; Peterson, Gibson and Dorcas, 1993). If temperatures rise they must retreat to burrows, before the temperatures exceed the individuals' critical thermal limits (CT_{max}), which in turn would reduce time available for acquiring energy for growth and reproduction (Sinervo *et al.*, 2010). Hence, reptiles are vulnerable to rising temperatures. Some authors have suggested that if the current warming trend continues, 30% of lizard species will be extinct by 2080 (Sinervo *et al.*, 2010). Additionally, reptiles' low rates of dispersal across anthropogenically fragmented landscapes will increase their risk of extinction (Meiri *et al.*, 2013; Paaijmans *et al.*, 2013).

In the search for new optimal environments, species' distributions will change, and regardless if such shifts occur across latitude or altitude, they will create new interspecific relationships and alter species composition within communities. A study on Mexican lizards found that the movement of lowland species to higher habitats could create competitive exclusion of highland species, thereby increasing the risk of extinction of those populations (Sinervo *et al.*, 2010). Some studies in temperate regions have found that due to the changing environmental temperatures, poleward range shifts of reptiles have occurred or are underway (Moreno-Rueda *et al.*, 2012; Wu, 2016b, 2016a). However, for the most of the temperate species the outlook of future projections is bleak. Based on climatic modelling, it has been estimated that at least 40% of reptile species will lose more than 90% of their range by 2050 (Warren *et al.*, 2018). For the most diverse Australian lizard group, the skinks, models predict range contractions for 71% of skink species by 2050 (Cabrelli and Hughes, 2015).

However, range shifts at the intraspecific level could vary geographically. Lizards' thermal tolerance differ between populations and among individuals within populations (Artacho, Jouanneau and Le Galliard, 2013; Bestion, Clobert and Cote, 2015). This variation could lead to differential patterns of dispersal between and within populations. Some phenotypes may be less adapted to changing local environmental conditions and may incur reduced fitness or may have a higher propensity to disperse (Clobert *et al.*, 2009; Meylan *et al.*, 2009). A study on

European common lizards (*Zootoca vivipara*) found that individuals with a lower thermal preference dispersed more from warmer than from cold habitats, while those with a higher thermal preference had a higher propensity to disperse from cold habitats (Bestion, Clobert and Cote, 2015). Hence it is important to consider intraspecific variation in the study of species' responses to climatic changes (Dytham *et al.*, 2014).

Reptiles may also adjust their activity budgets to avoid death from overheating when thermoregulation fails to keep body temperature within operative ranges (Sinervo *et al.*, 2010). Retreating to burrows or remaining inactive reduces the time available for foraging, which can lead to a decrease in the acquisition of resources required for growth and reproduction. Such changes can reduce fecundity or fitness of females, increasing the risk of local extinctions (Sinervo *et al.*, 2010). On the other hand, reptile populations inhabiting colder regions can extend their activity periods and reproduction due to warming. Despite these benefits, extreme heat for which these species are not adapted could also affect individual fitness (Sinervo *et al.*, 2010; Levy *et al.*, 2016).

1.4. Embryonic stages and nest selection in reptiles

The embryonic stages of oviparous reptiles is a critical part of their life history, as egg development occurs in unattended nests, which are vulnerable to predation and thermal variation. Unlike adults, embryos cannot thermoregulate, and so are vulnerable to thermal spikes during heatwaves (Du and Shine, 2015; Levy *et al.*, 2015). High nest temperatures pose a risk for reptiles because incubation temperatures affect offspring phenotypes such as sex, body size, mass, time of hatching, and behaviour (Deeming, 2004; Mainwaring *et al.*, 2017; Noble, Stenhouse and Schwanz, 2018). Therefore, spatial variation in nest temperatures can affect the geographic distribution of species (Evans, Diamond and Kelly, 2015; Levy *et al.*, 2015). Studying the responses of embryos to incubation temperatures in a warming environment is crucial for predicting future distributions, but we lack detailed studies on this topic (Kearney and Porter, 2004; Kearney, Wintle and Porter, 2010). In addition, determining locations where conditions are suitable for embryo development is crucial for knowing where the species may disperse to, which is crucial for planning assisted colonization of threatened species (Mitchell *et al.*, 2016). Currently, we know little about how females and embryos will respond to future changes in nest temperatures.

The vulnerability of embryos to high temperatures means that nest-site selection can influence the fitness of both offspring and mothers. Therefore, selection may favour those individuals that select better microclimates for their eggs (Pike, 2013). In this sense, not only is the physical structure of the nests important, but the nest location dictates the amount of sunlight, moisture, wind, and other factors that could affect the nests microclimate. In temperate regions, animals select sites to lay their eggs with a thermal regime that heats faster and cools slower than the surrounding environment (Rockweit *et al.*, 2012). Some studies on lizards have found that females select nest sites from the available habitats based on that microclimatic conditions that ensure optimal development (Pike, Webb and Shine, 2010; Mitchell *et al.*, 2016). Now, with global climate change, nest temperatures (and their thermal regime variance) are predicted to increase, potentially impacting hatchling phenotypes and fitness (Kearney and Porter, 2004, 2009; Pearson and Warner, 2018). Noble, Stenhouse and Schwanz (2018) in a formal meta-analysis review, identified three key pathways in which future temperatures would affect populations: phenology, hatchling success and post-hatching phenotypic effects. Hence the need for adaptability on nest site selection behaviour in order to avoid population extinction (Mainwaring *et al.*, 2017). There is a knowledge gap on how females select their nests under different geographic and environmental conditions, and the degree of plasticity in nest site selection.

Selecting an appropriate nesting location is critical for maternal fitness because it affects offspring survival directly (via egg survival) and indirectly (via phenotypic variation). In addition, maternal oviposition behaviour can affect maternal fitness by affecting a females' to exposure to predation (Refsnider, 2016). In reptiles, several drivers can influence maternal nesting decisions: maximizing offspring survival; maximizing female survival; modifying offspring phenotype; proximity to optimal habitats for hatchlings survival; maternal effect of philopatry; and copying other females' choices (Refsnider and Janzen, 2010). Research on nest-site selection can help us to understand these drivers, and by informing us about the outcomes of the different nesting behaviours, can help us to manage populations (Refsnider, 2016). From the female's perspective, nest-site selection involves balancing different drivers and their outcomes. Some drivers may seem maladaptive when studied separately, and should be studied in the context of the species' environment to understand how and why individuals choose nest sites (Streby, Refsnider and Andersen, 2014).

Some reptile species have temperature-dependent sex determination (TSD), in which the mean temperature during embryonic development determines the sex of the offspring (Bull, 1980). Therefore thermal variation can also affect populations of species with TSD, by changing sex ratios, as it has already been reported in populations of sea turtles (Mitchell and Janzen, 2010; Laloë *et al.*, 2014, 2017). Some of these variations might be even beneficial in terms of population survival. For example, Laloë *et al.*, 2014 showed that global warming could increase the population size of some sea turtles by increasing the number of females, and thus egg production. Yet, if the trend continues for several generations, populations could suffer demographic collapse due to extremely biased development of one sex (Laloë *et al.*, 2017).

Nevertheless, researchers found that some species compensate for climate change via maternal nest site selection. For instance, a study on Australian water dragons (*Itellagama lesueurii*) found that females select more open nest sites with higher incident radiation in colder regions, but lay eggs in shadier nests in hotter regions (Doody, Guarino, George*s, et al*., 2006). Mean nest temperatures differed across the range, but were not influenced by mean monthly maximum air temperatures or mean monthly soil temperatures (at 10 cm depth), suggesting that females compensated for climatic variation when choosing nesting locations (Doody, Guarino, Georges, *et al.*, 2006). Such plasticity in nest site selection can effectively buffer populations from increasing temperatures. However, such changes are not universal. For example, females from some populations of the Australian eastern three-lined skink (*Acritoscincus duperreyi*) reduced nest depth under warmer temperatures while nesting, which would increase the risk of offspring experiencing lethal temperatures predicted under climate change scenarios (Telemeco *et al.*, 2017). Plasticity then can mitigate some impacts of rising temperatures, but not all of them.

1.5. Range shifts

To study the effects of the rising temperature on a species, species distribution models can help to predict future geographic ranges. The natural distributional range comprises the defined space in which species occur and there are two main approaches for estimating it: correlative (or statistical) and mechanistic (or physiological) species distributional models (SDMs) (Kearney and Porter, 2009). These models serve two main purposes, interpolation or extrapolation. For the first, training data is used to predict novel areas where the species could be found, both within the same range of the sampled environments and the sampling time frame (Elith and Leathwick, 2009). Interpolation can be used to analyse species distributions on global scales; visualize species scarcity across a defined region for management or conservation; or for depicting new suitable areas for uncommon species without major theoretical risks (Guisan and Thuiller, 2005). On the other hand, extrapolation or forecasting can predict occurrences outside the sampled geographic space and/or over different periods (past or future environmental conditions). Then, analyses such as range predictions under climate change use extrapolation to assess species ecological processes (Araújo and New, 2007; Elith and Leathwick, 2009). Even though both types of modelling differ in their theoretical approaches, and have advantages and disadvantages, they are still widely used and can produce similar results when predicting species ranges (Kearney, Wintle and Porter, 2010).

Correlative SDMs are more commonly used because they use easily available data and have been proven to predict species range with a good precision (Elith and Leathwick, 2009). These kinds of SDMs are based on the Hutchinsonian environmental hyperspace of a species and take environmental variables and geographical space out of the occurrence or abundance data. Then, by different algorithms they implicitly calculate the species range (Kearney, Wintle and Porter, 2010), with the key assumptions of sufficient environmental gradient sampling, and species–environment equilibrium (Elith and Leathwick, 2009). Future climatic variations pose a risk when using these models, because the key assumptions would not be met, as new environmental spaces will be created via changes in climate, and species-climate relationships could work in different ways (Kearney and Porter, 2009; Kearney, Wintle and Porter, 2010). In spite of this risk, researchers are still using these models to infer shifts in species range under the different climate change scenarios (e.g. Pike, 2014; Cabrelli and Hughes, 2015).

Mechanistic SDMs incorporate predictive variables that explicitly account for ecological processes that shape species' distributions such as morphology, physiology and behaviour (Kearney, Wintle and Porter, 2010; Mitchell *et al.*, 2016). They work on the premise that microhabitat conditions are the link through which climate and physiological constraints of organisms connect (Kearney, Isaac and Porter, 2014). Some authors have stated that mechanistic models work better at predicting climate change impacts because they include species physiological processes already established (Elith, Kearney and Phillips, 2010), are independent of species inter- and intra-specific interactions and of occurrence data (Mitchell *et al.*, 2016). However, the disadvantages of using these models is that they include no estimation of uncertainty, and it is difficult to acquire data for determining key processes limiting physiological thresholds of organisms (Kearney and Porter, 2009; Kearney, Wintle and Porter, 2010; Mitchell *et al.*, 2016).

1.6. Current knowledge gaps

While we know how some lizard species choose their nest sites, we do not know if females can adjust their nest site choices to track changing environments. One way to examine this question is to see whether there is geographic variation in nest characteristics and temperatures across a species range. If females adjust their behaviour to match local conditions, and select sites with optimal temperatures, we should see little variation in mean nest temperatures across a species range. Another gap in our knowledge is the range of microhabitat conditions that lizard embryos can endure, and how embryos might respond to future changes in climate (Kearney *et al.*, 2014). With this in mind, if we identified sites with optimal thermal conditions for embryogenesis, we could predict future ranges of species with more certainty, or use such information for assisted colonisation. Finally, although widespread common species are often overlooked in favour of rare species, range loss in widespread species could affect numerous species via changes in competitive interactions or trophic cascades (Warren *et al.*, 2018).

1.7. Velvet gecko as a model species

The velvet gecko (*Amalosia lesueurii*) is a nocturnal lizard with a large geographic range that comprises the eastern coast of Australia, from southeastern New South Wales to southeastern Queensland (Figure 3, Cogger, 2014). This species is abundant and well-studied, which makes it a good model to work with. The geckos forage at night on the open rock faces, or among ground litter at the edges of the rock faces (Cogger, 2014). They select sun-exposed rocks as diurnal indirect thermoregulatory sites on sandstone rock outcrops (Webb, Pike and Shine, 2008, Figure 4) and actively thermoregulate within diurnal shelter sites by indirect basking (Schlesinger and Shine, 1994).

Figure 3. Distribution of *A. lesueurii* (Cogger, 2014).

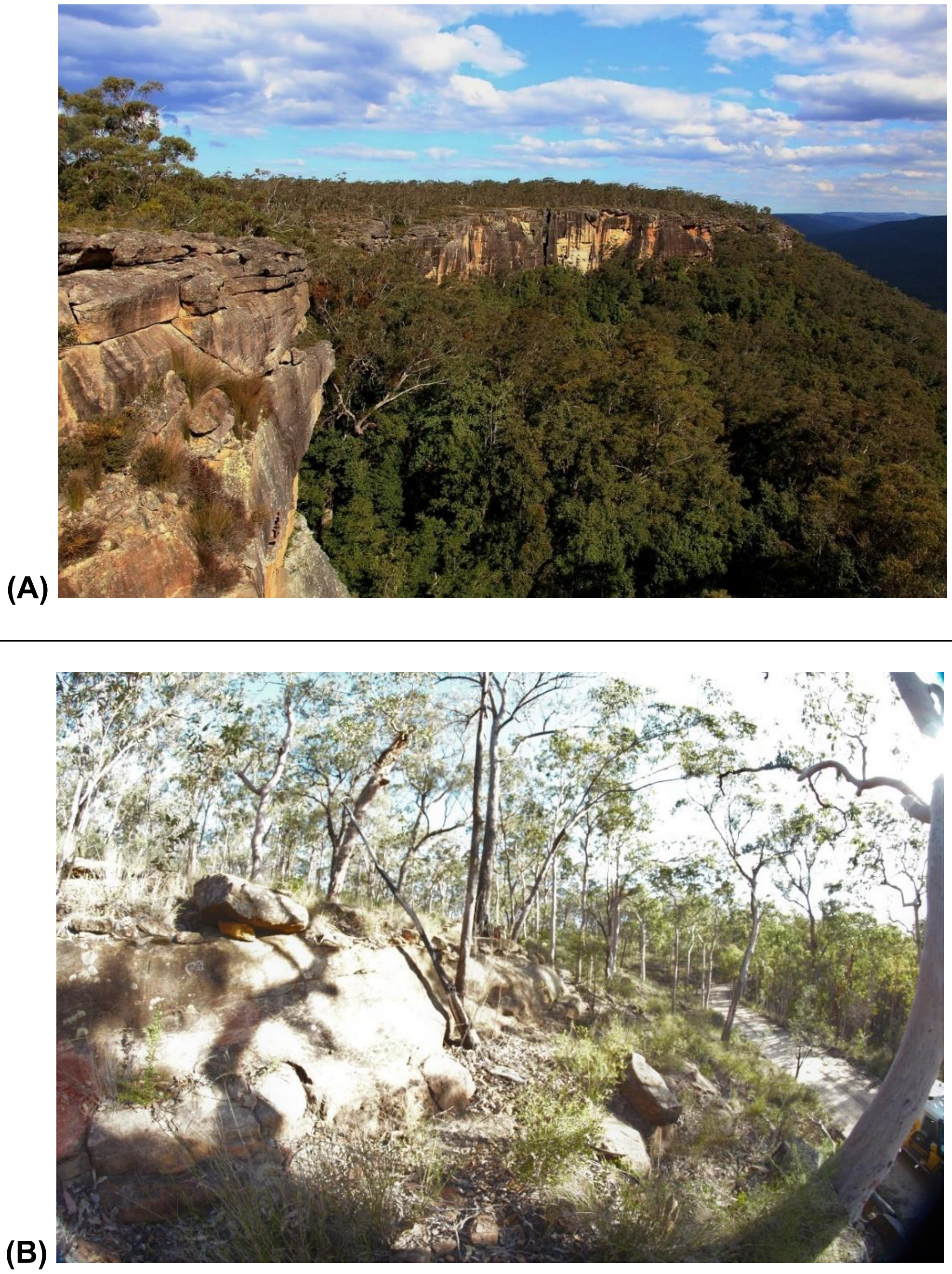


Figure 4. Sandstone plateaus, habitat of the velvet gecko (*Amalosia lesueurii*). (A) Morton National Park, NSW. (B) Yengo National Park, NSW.

Females lay two parchment-shelled eggs in communal nests in rock crevices on sandstone outcrops (Bustard, 1967; Webb, Pike and Shine, 2008; Figure 5). Females select nest sites with specific structural characteristics (e.g. crevice depth, canopy cover, direction of entrance) and thermal properties (Pike, Webb and Shine, 2010; Pike, Webb and Andrews, 2011). Dayananda et al. (2016) found a strong positive correlation between maximum daily air temperatures and daily mean and maximum nest temperatures (Figure 6). Additionally, laboratory experiments found that eggs incubated under ‘future’ temperature regimes produced smaller hatchlings that were slower, and had poorer spatial learning abilities, and lower survival than hatchlings from current nest temperature regimes (Dayananda *et al.*, 2016; Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017). Genetic studies suggest that velvet geckos have poor dispersal (Dubey *et al.*, 2012) which coupled with the isolated habitats where *A. lesueurii* lives, may render populations more vulnerable to extinction. In addition, as the species has a ‘slow’ life history, so factors that increase mortality rates of hatchlings or adults will increase the risk of extinction (Webb, Pike and Shine, 2008).

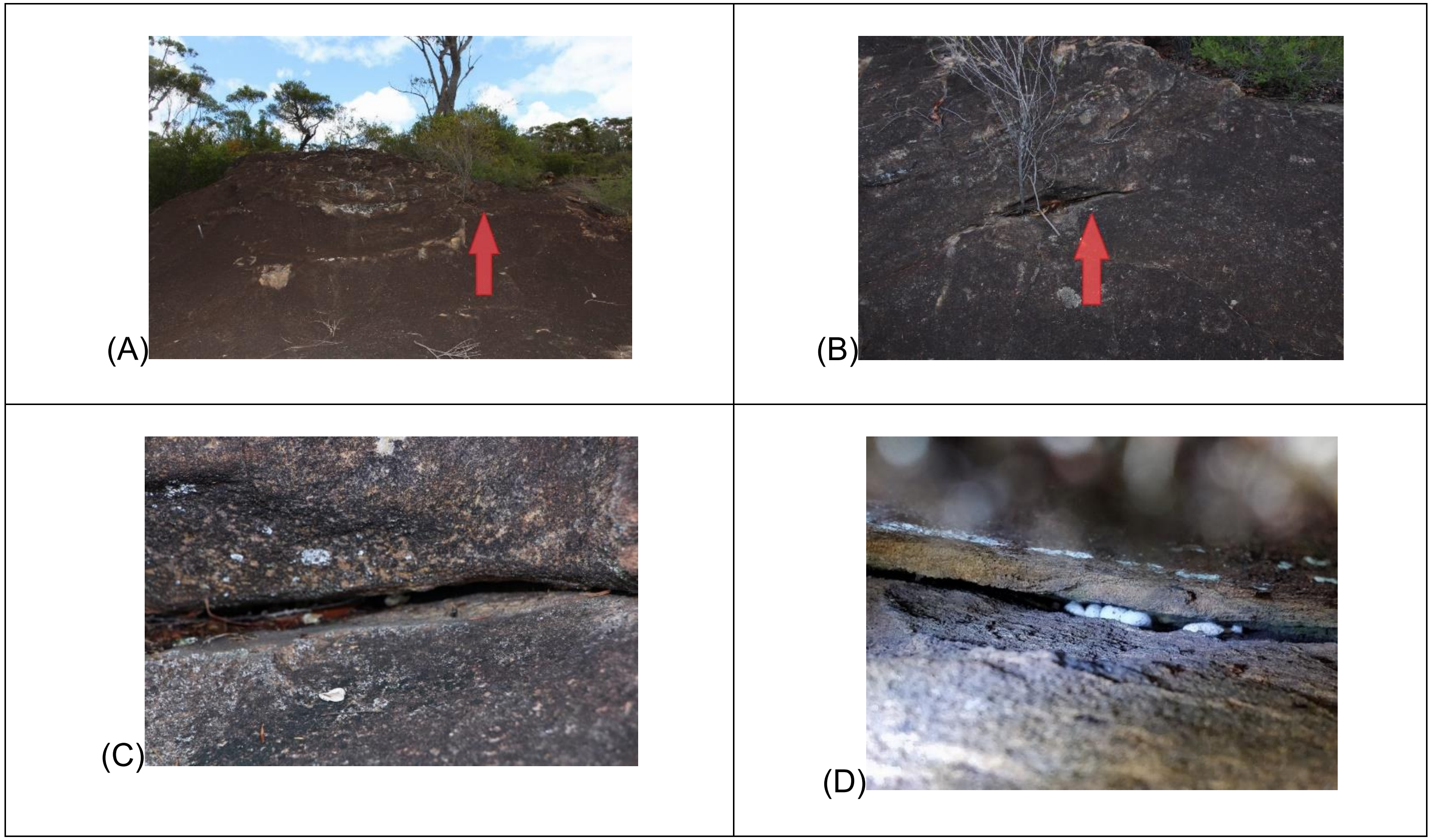


Figure 5. Usual configuration of the nest of *A. lesueurii* at Dharawal National Park. Showing nests from general sandstone habitat to detailed crevice nest from A to D.

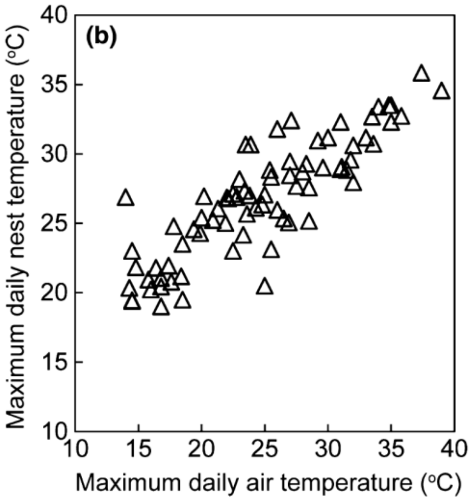


Figure 6. Correlation between air and nests temperatures (modified from Dayananda *et al.* 2016).

1.8. Aims of the study

The broad aim of my study is to investigate the effects of climatic changes on the Australian endemic, widely distributed and abundant velvet gecko (*Amalosia* lesueurii). If temperatures keep rising as predicted by climate models, and there is a strong positive correlation between nest temperatures and air temperatures (Dayananda *et al.,* 2016), then temperatures inside nests of this species will increase, which might affect the viability some populations. To investigate whether females show plasticity in nest site selection that might buffer populations from potential future increases in temperature, I carried out a field study of nest sites. I measured the canopy cover and sunlight radiation above nests, their physical structure, and the temperatures within the nests. I examined these variables in two populations: one from the southern edge of the species geographic range, and another in the middle of the species range. Additionally, I modelled the species distribution under current climate and future climate projections to understand if future climates will be suitable for the species. Keeping in line with these goals, I addressed five broad questions:

- Can phenotypic plasticity buffer populations from rising temperatures?
- Do nest-site selection features and temperatures vary between geographically distant populations?
- What is the climatic suitable area for the species under current climate?
- What bioclimatic variables define species distribution?
- How will the species distribution change with future climate?

1.9. Thesis structure

The thesis consists of a series of papers that I plan to submit to journals for consideration for publication. In **Chapter 2,** I investigate whether there is geographic variation in the thermal regimes, physical structure and light conditions of velvet gecko nests. To do this, I compare nest site characteristics in two geographically distant populations. In **Chapter 3,** I describe the species distribution model that I constructed for my study species, the environmental space of the species, and the climatic variables that define the species range. Additionally, I estimate the impacts of rising temperatures under a set of future climatic scenarios, and I discuss the range loss and the movements of the species. **In Chapter 4,** I provide my general conclusions and a critical general review of my results, and discuss some further directions for future research.

1.10. Ethics and permits

All the experiments and methods presented in this thesis were conducted according to the code of practice for the care and use of animals for scientific purposes. All procedures were approved by the University of Technology Sydney Animal Care and Ethics Committee (protocol # ACEC ETH16-0722). All fieldwork was carried out according to the New South Wales National parks and Wildlife act under the scientific licence SL101982, issued under the Biodiversity Conservation Act 2016. Additionally, I obtained conditional consent under clause 23(2), of the National Parks and Wildlife Regulation 2009 to enter and undertake research in Royal National Park.

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Chapter 2. Geographic variation in nest site selection in the velvet gecko (*Amalosia lesueurii*)

2.1. Abstract

Nest site choice directly affects egg hatching success, hatchling survival and thus parental fitness. Many species of lizards lay their eggs inside shallow nests in exposed areas so that nest temperatures may fluctuate in response to local weather conditions. During heatwaves, temperatures in nests may spike, potentially exposing embryos to stressful thermal conditions. Whether reptiles can respond rapidly to climatic change via plasticity in nest site selection is an open field of research. By studying latitudinal variation in nest-site choice in species with broad geographic ranges, we can evaluate whether females have the capacity to modify their nest-site choices in response to changes in temperature. I investigated geographic variation in nest site selection in the velvet gecko (*Amalosia lesueurii*), a widely distributed and abundant lizard species. I examined thermal regimes, physical structure and incident light variables of nests in two populations (Morton National Park and Yengo National Park), encompassing more than 25% of the species range. I found strong positive correlations between air temperatures and nest temperatures, with temperatures in some nests exceeding the species' critical thermal maximum during summer heatwaves. The species also showed variation between the two populations in the physical structure, incident light and thermal characteristics of nest sites, so that mean nest temperatures did not differ between locations. My results show that females can adjust nest-site choice to suit local environments, but nests in the northern population experienced higher temperatures during heatwaves than

nests in the southern population. Future research could clarify whether exposure to high temperatures influences hatching success or offspring phenotypes.

2.2. Introduction

Oviposition site choice can directly impact egg hatching success, the performance and survival of hatchlings, and parental fitness (Bernardo, 1996; Resetarits, 1996). Most lizards do not care for their eggs, and incubation periods often extend for several months (Shine, 2005). This means that eggs deposited inside nests are subject to external pressures including predation, disease, and thermal stress (Du and Shine, 2015). Numerous laboratory studies have found that incubation temperatures can influence a multitude of offspring traits, including body size, sex, time of hatching, and rates of survival (Dayananda *et al*., 2016; Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017; Laloë *et al*., 2017; Noble, Stenhouse and Schwanz, 2018). Many lizards lay eggs inside shallow nests in exposed areas, and nest temperatures may fluctuate in response to local weather conditions (Shine and Elphick, 2001). Thus, during summer heatwaves, nest temperatures may experience thermal spikes, which in turn may affect hatchlings' survival (Dayananda *et al.*, 2016; Dayananda and Webb, 2017; Abayarathna, Murray and Webb, 2019). The long incubation periods of many lizard species increases the likelihood that embryos may experience lethally high temperatures during heatwaves, which may affect population viability (Levy *et al.*, 2016; Mitchell *et al.*, 2016).

Maternal nest site choice is a key mechanism by which females can influence phenotypic traits and survival of offspring (Refsnider and Janzen, 2010). To combat increasing temperatures, females can buffer their embryos from high temperatures by carefully selecting suitable sites for embryo development (Durant *et al.*, 2013; Pike, 2013). Despite its importance, few studies have examined whether reptiles can respond rapidly to climatic change via plasticity in nest site selection. One way to tackle this question is to study nest site selection in species with broad geographic ranges. Species with broad geographic ranges are likely to experience marked latitudinal differences in temperatures of potential nest sites. Females could compensate for this variation by either nesting earlier at hotter sites, or by digging deeper nests, or choosing shadier nest sites at hotter locations. For example, in the eastern water dragon (*Itellagama lesueurii)* nest depth did not differ across latitude, but females selected nest sites with higher canopy openness at cooler sites, and sites with lower openness at warmer sites (Doody, Guarino, Georges, *et al.*, 2006). Thus, by examining variation in nest-site choice across a species range, we can evaluate whether females have the capacity to modify decisions in response to changes in temperature or other environmental conditions. Such information is crucial for determining how future changes in temperature may affect offspring performance and fitness, and ultimately, the persistence of populations (Refsnider, 2016; Mainwaring *et al.*, 2017).

In the present study, I investigated nest site selection in two geographically distant populations of the velvet gecko (*Amalosia lesueurii*). This species has a broad geographic range, from southern New South Wales (NSW) through to southern Queensland (QLD) in eastern Australia (Cogger, 2014). Across the species geographic range, females lay eggs communally inside rock crevices, and nest temperatures are influenced by ambient temperatures. Laboratory studies have shown that higher incubation temperatures produce smaller hatchlings with lower survival (Dayananda *et al.*, 2016). Thus, if females select sites to maximise offspring fitness, I would expect that they would modify their nest-site choice to provide optimal temperatures for developing embryos. That is, nests from colder southerly latitudes should be more open than nests from hotter northern latitudes, whereas both mean and maximum nest temperatures should be similar across latitudes. To investigate variation in nest site choice, I measured the physical attributes and temperatures of communal nests and available nest sites from two populations. I selected two study sites in eastern NSW: a southern population in Morton National Park and a population 215 km north, near Yengo National Park.

2.3. Materials and methods

2.3.1. Study species

The velvet gecko (*Amalosia lesueurii*) is a nocturnal lizard with a large geographic range that comprises the eastern coast of Australia, from south-eastern NSW to south-eastern QLD (Cogger, 2014). Geckos select sun-exposed rocks as diurnal shelter sites on sandstone rock outcrops (Webb et al. 2008) and actively thermoregulate within diurnal shelter sites by indirect basking (Schlesinger and Shine, 1994). Females reproduce once a year in spring, and lay two parchment-shelled eggs in communal nests in rock crevices on sandstone outcrops (Bustard, 1967; Webb, Pike and Shine, 2008). In a southern population (Morton National Park), researchers found that females selected nest-site crevices with specific structural and physical characteristics (e.g. depth, shade, direction of entrance), and which differed from other rock crevices available in the habitat (Pike, Webb and Shine, 2010; Pike, Webb and Andrews, 2011). In the laboratory, females were more likely to lay eggs in crevices with hatched egg shells than empty crevices, suggesting that females used social cues to select appropriate nest sites. Incubation experiments showed that eggs incubated under ‘future’ temperature regimes (mean = 27°C, range = 14 – 37°C) produced smaller hatchlings that had lower survival than hatchlings from current nest temperature (mean = 23.2°C, range = 10 – 33°C) regimes (Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017).

2.3.2. Nest sites

I searched for nest sites in the species southern range in Morton National Park and 215 km north in Yengo National Park where the species is abundant (Figure 7). The maximum distance between sites was 230km, so I covered approximately 25% of species latitudinal range (Cogger, 2014).

Figure 7. Study sites. Blue mark point: Yengo National Park; yellow mark point: Morton National Park; green area: species' range.

2.3.3. Nest site attributes

I looked for nests on rock outcrops during the 2018 nesting season (September-November). With the aid of a head torch, I searched inside rock crevices for active nests that contained fresh eggs or white eggshells. Once I located a nest, I marked its position with a GPS, and recorded the nest depth (distance between crevice entry and deposited eggs), the height and width of the crevice entrance, and the thickness of the overlying sandstone above the crevice (TH). I also recorded the direction of the crevice entrance with a compass. To measure nest temperatures, I placed a miniature temperature data logger (Thermochron iButton, factory calibrated and accurate to 0.5°C) inside each nest beside freshly laid eggs or eggshells from the previous nesting season. In order to retrieve the data loggers, I wrapped them in wire and parafilm, as has been done before in previous studies (Figure 8). I counted any eggs present in the nest, and also recorded the number of white and brown eggshells (Webb, Pike and Shine, 2008; Pike, Webb and Andrews, 2011).

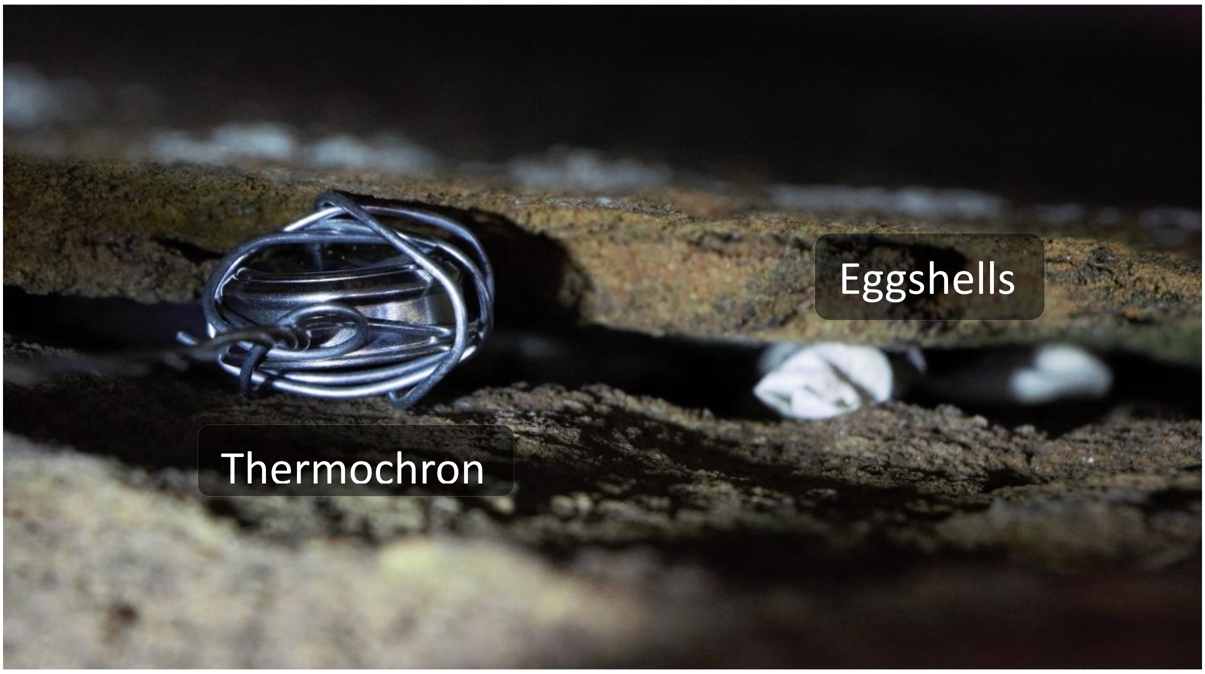


Figure 8. Photo of the inside of a nest with the deployed Thermochron IButton next to the eggshells.

To compare temperatures of gecko nests with those inside nearby crevices, I deployed 77 data loggers (iButtons) inside nests and crevices in November 2018. Data loggers were programmed to record temperatures at 30 minutes intervals. Twelve loggers failed, or were found outside of crevices, so the final sample size was 65. I obtained thermal data for 33 crevices and 15 nests from Morton, and

11 crevices and 6 nests from Yengo. Temperature records spanned 98 days from the 23rd of November 2018 until the 28th of February 2019, and so covered the incubation period for my study species (80 – 120 days; Doughty, 1997).

Canopy cover limits incidental solar radiation on rock outcrops, and directly affects microhabitat temperatures (Pringle, Webb and Shine, 2003). I used hemispherical photography and the software Gap Light Analyser (GAP, Frazer *et al.*, 1999) to analyse canopy cover and sunlight penetration at nest sites and crevices. I took photos on top of each nest and random crevice with the camera facing the magnetic north (measured with a compass), with a canon 7D camera fitted with an 8 mm fish-eye lens with a fixed diagram aperture and the focus set to infinity. For each photo, I entered the coordinates, elevation, and noted if there were structures blocking sunlight from entering the nest or crevice. Solar time was set to 1 minute, growing season was set to the incubation period of the species (November to February), sky region was set to 40 and 10, the data source was set on modelled, the solar constant was kept as default (1367), sky region brightness was selected as UOC, clear-sky transmission coefficient was set to 0.65, and I selected MJ/m2/d as units (Doody, Guarino, Harlow*, et al.*, 2006). I calculated the cloudiness index and the spectral fraction and beam fraction with the average monthly day length and average daily sunshine retrieved for each point (nest or crevice) from the Australian Bureau of Meteorology (Bureau of Meteorology, no date) as follows:

Cloudiness index (*Kt*):

$$\frac{H}{Ho} = 0.18 + 0.62\left(\frac{n}{Nd}\right) = Kt$$

Spectral fraction (Rp/Rs):

$$\frac{Rp}{Rs} = 1^{-\left(-0.499Kt^{-0.219}\right)}$$

Beam Fraction (*H6/H*):

$$\frac{H6}{H} = 1^{-\left(-3.044\mathrm{Kt}^{2.436}\right)}$$

With Nd and N as:

Nd = average monthly day length

N = average daily sunshine

The software returns a set of variables from which I used three for the analyses. Percentage of canopy openness (%CO) that accounts for the open sky that can be seen from beneath the canopy; percentage of site openness (%SO) which also calculates the open sky visible from beneath the canopy but calculated given the additional influence of topographic shading; and percentage of trans total (%TT), or the total amount of solar radiation (direct and diffused) that gets to the nests through the canopy (Frazer, Canham and Lertzman, 1999).

2.3.4. Available nest sites

For each nest, I selected 1 to 5 random crevices within 20 m of the nest. For each crevice detected, I measured the same variables as for the nests (see above). In total, I measured attributes of 15 nests and 33 crevices in Morton, and 6 nests and 11 crevices in Yengo.

2.3.5. Statistical analyses

Prior to statistical analyses, I first tested for correlation between variables. I tested whether variables met the assumptions of normality and homogeneity of variances using Shapiro-Wilk and Levene's test respectively (Table 1). When it was necessary to meet the assumptions, I log-transformed raw measures prior to analysis. I ran two-way ANOVAs with site and crevice type as the factors, and depth, width, height, sandstone thickness above crevice and the percentage of trans-total solar radiation as independent variables. Despite numerous data transformations for %CO and %SO, they did not meet the assumptions so I ran Kruskal-Wallis independent tests with site and crevice type as factors, and canopy openness, and site openness as dependent variables (Pike, Webb and Shine, 2010; Pike, Webb and Andrews, 2011).

Table 1. Normality and homogeneity of variances tests for physical structure and incident light variables of nests and crevices.

	Levene's test				**Shapiro-Wilk**			
Variable	Levene Statistic	df1	df2	Sig.	Site	Statistic	Df	Sig.
%TT	2.420	3	73	0.073*	Morton	0.767	55	0.000
					Yengo	0.948	22	0.291**
%SO	4.874	3	73	0.004	Morton	0.859	55	0.000
					Yengo	0.911	22	0.049**
%CO	4.853	3	73	0.004	Morton	0.860	55	0.000
					Yengo	0.909	22	0.044**
TH	0.213	3	67.600	0.887*	Morton	0.979	55	0.450**
					Yengo	0.949	22	0.304**
Height	1.695	3	68.790	0.176*	Morton	0.904	55	0.000
					Yengo	0.946	22	0.259**
Width	2.518	3	68.675	0.065*	Morton	0.973	55	0.242**
					Yengo	0.923	22	0.087**
Depth	0.352	3	68.628	0.788*	Morton	0.987	55	0.818**
					Yengo	0.961	22	0.500**

*null hypothesis of homogeneity of variances not rejected.
**null hypothesis of normal distribution not rejected.

To test whether daily nest temperatures differed between locations (Morton vs Yengo), and between nest sites and crevices, I used a two-factor repeated measures ANOVAs with location and crevice type as the factors, and daily temperatures (minimum, mean and maximum; analysed separately) as the repeated dependent variables. To determine whether air temperature influenced nest temperatures, I downloaded data for the nearest weather stations (Nowra Ran Air Station AWS, station number 68072, for Morton, and Richmond RAAF base, station number 067105, for Yengo) from the Bureau of Meteorology. I then carried out Pearson correlations to see if daily temperatures were correlated with air temperatures. Because prolonged exposure to high temperatures may negatively affect embryos (Telemeco *et al.*, 2017), I calculated the number of hours during which nest temperatures exceeded 39.9°C, the species Critical Thermal Maxima (CT$_{max}$; Abayarathna, Murray, & Webb, 2019). For both types of analysis, the thermal regime and the nest site features, I also compared each simple effect of the combinations between each factor as an ad-hoc test. I ran statistical tests in SPSS version 25 (see Figure 9).

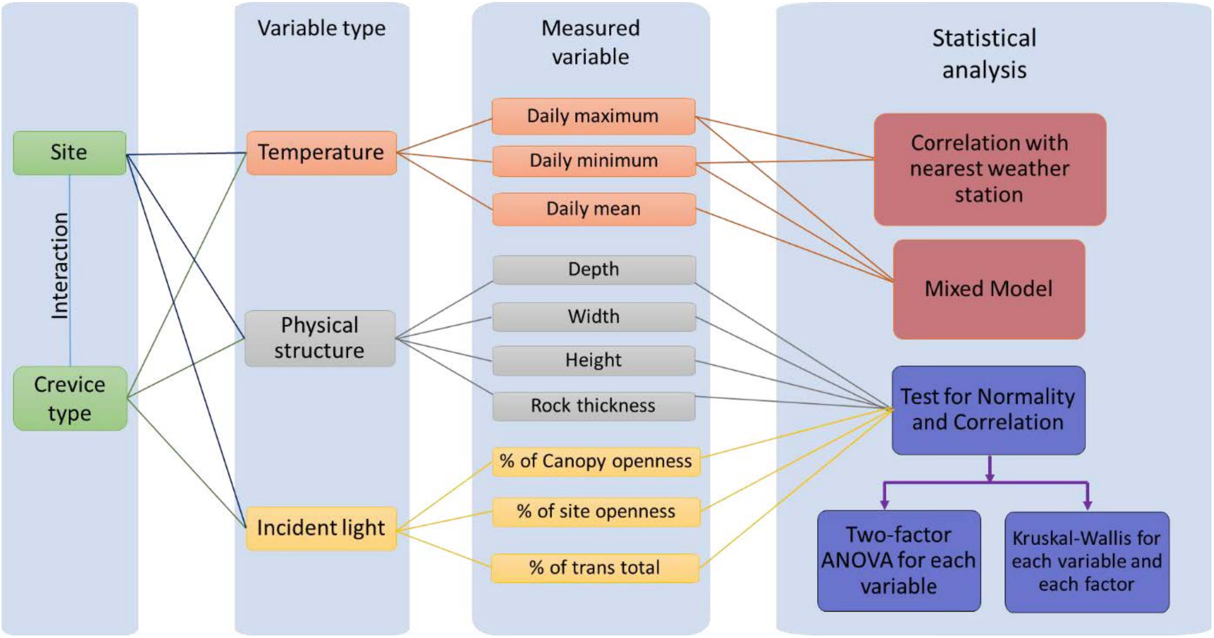
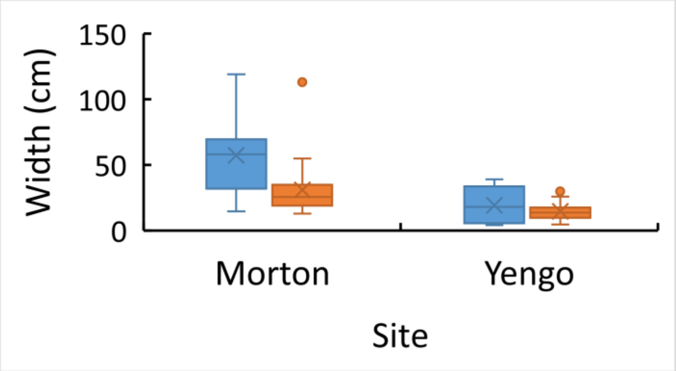


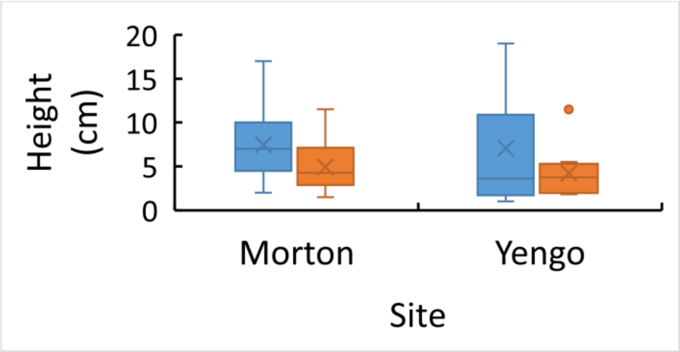
Figure 9. Statistical analyses performed on this study specifying the paths followed for each factor, and each type of variable.

2.4. Results

2.4.1. Physical structure and incident light

Physical structure, and incident light variables were positively correlated (Table 2, Table 3). Nests were deeper, wider and had thicker rocks above them in Morton than Yengo ($F_{(3,73)} = 32.85$, $p = 0.000$; $F_{(3,73)} = 43.66$, $p = 0.000$; $F_{(3,73)} = 4.99$, $p = 0.028$ respectively). However, I found no differences in height between sites ($F_{(3,73)}= 3.81$, $p= 0.055$). Crevices were wider than nests at both sites ($F_{(3,73)} = 6.832$, $p = 0.011$). Crevices and nests did not differ in any of the other physical structural variables at either site (depth: $F_{(3,73)} = 0.38$, $p = 0.54$; height: $F_{(3,73)} = 2.20$, $p = 0.14$; TH: $F_{(3,73)} = 0.16$, $p = 0.69$) and there was no interaction (depth: $F_{(3,73)} = 0.141$, $p = 0.709$; width: $F_{(3,73)} = 2.830$, $p = 0.097$; height: $F_{(3,73)} = 0.108$, $p = 0.743$; TH: $F_{(3,73)} = 0.053$, $p = 0.819$; see




Height (cm)
20
15
10
5
0
Morton
Yengo
Site

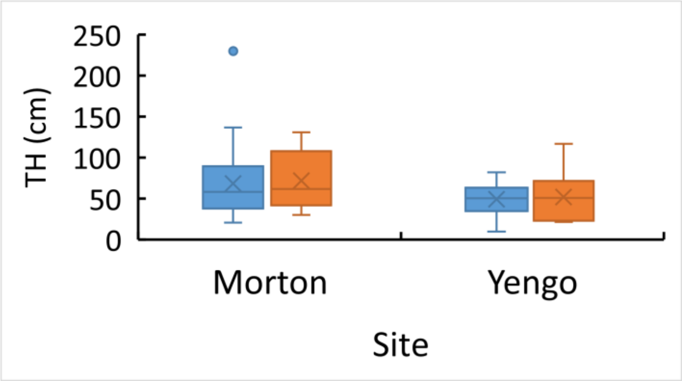

TH (cm)
250
200
150
100
50
0
Morton
Yengo
Site

Figure **10**).

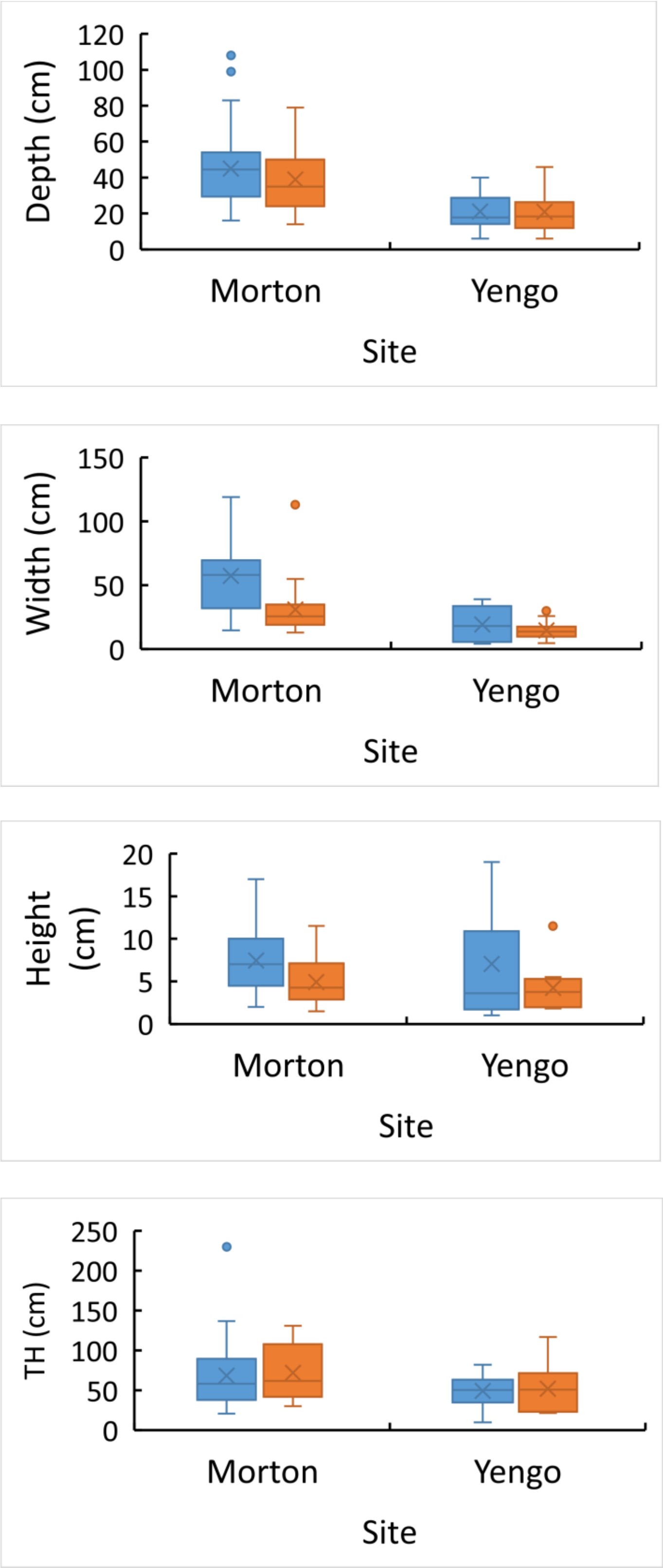


Figure 10. Boxplot of physical structure variables comparing sites and types of crevices. Orange: nests; blue: crevices.

Table 2. Pearson correlations between physical structure variables.

Pearson Correlations	**Depth**	**Width**	**Height**	**TH**
Depth	1	.577**	.337**	.248*
Width	.577**	1	.365**	.255*
Height	.337**	.365**	1	-0.046
TH	.248*	.255*	-0.046	1

****. Correlation is significant at the 0.01 level (2-tailed).**

***. Correlation is significant at the 0.05 level (2-tailed).**

Table 3. Pearson correlations between incident light variables.

Pearson Correlations	**%Canopy Openness**	**%Site Openness**	**% Trans Total**
%Canopy Openness	1	1.000**	.915**
%Site Openness	1.000**	1	.912**
% Trans Total	.915**	.912**	1

****. Correlation is significant at the 0.01 level (2-tailed).**

Morton presented a larger percentage of canopy openness, percentage of site openness and percentage of total solar radiation than Yengo ($H_{(chi^2)} = 21.27$, $p < 0.001$; $H_{(chi^2)} = 20.86$, $p < 0.001$; $F_{(3, 73)} = 8.830$, $p = 0.004$ respectively). Crevices and nests did not differ in any of the analysed incident light variables at any of the study sites (%CO: $H_{(chi^2)} = 1.811$, $p = 0.178$; %SO $H_{(chi^2)} = 1.72$, $p = 0.188$; %TT: $F_{(3, 73)} = 0.163$, $p = 0.688$) and neither was there an effect of the interaction of factors (%TT: $F_{(3, 73)} = 0.294$, $p = 0.590$; see Figure 11)

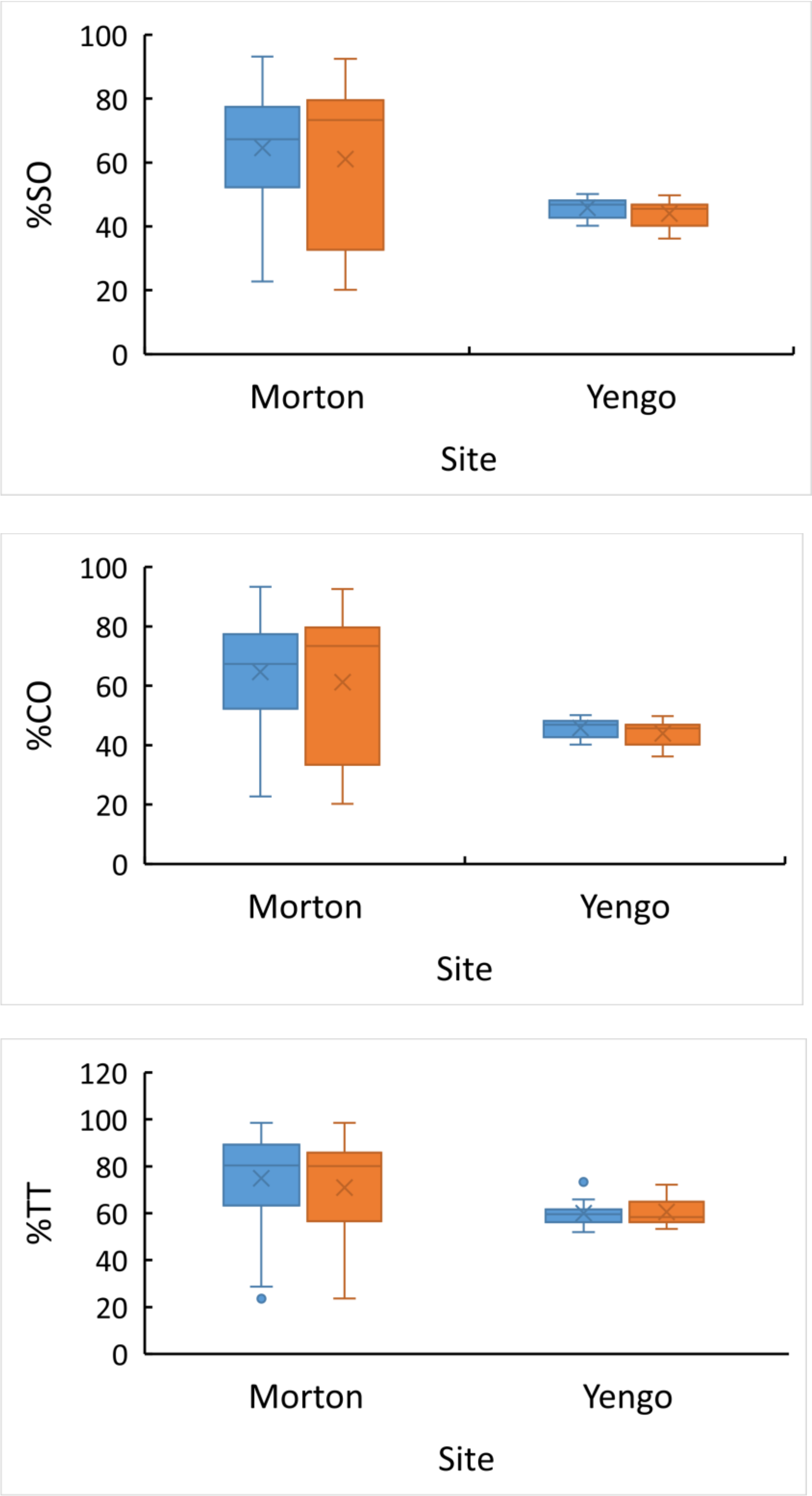


Figure 11. Boxplot for incident light variables comparing sites and types of crevices. Orange: nests; blue: crevices.

2.4.2. Thermal regime

Temperatures fluctuated throughout the incubation period, but the temporal patterns were similar at both sites. That is, both sites experienced heatwaves with temperature peaks above 35°C and cold snaps at similar times. In general, Yengo was colder and hotter, and experienced lower minimum and higher maximum daily temperatures, than Morton. Minimum daily temperatures differed during the incubation period (see Figure 12; $F_{(1,97)} = 951.2$, p = 0.000), and between sites ($F_{(1,58)} = 16.658$, p = 0.000), but not between types of crevice (see Figure 13**,** Figure 14; $F_{(1,58)} = 0.524$, p = 0.472), nor for the interaction of both factors ($F_{(1,58)} = 2.282$, p = 0.136).

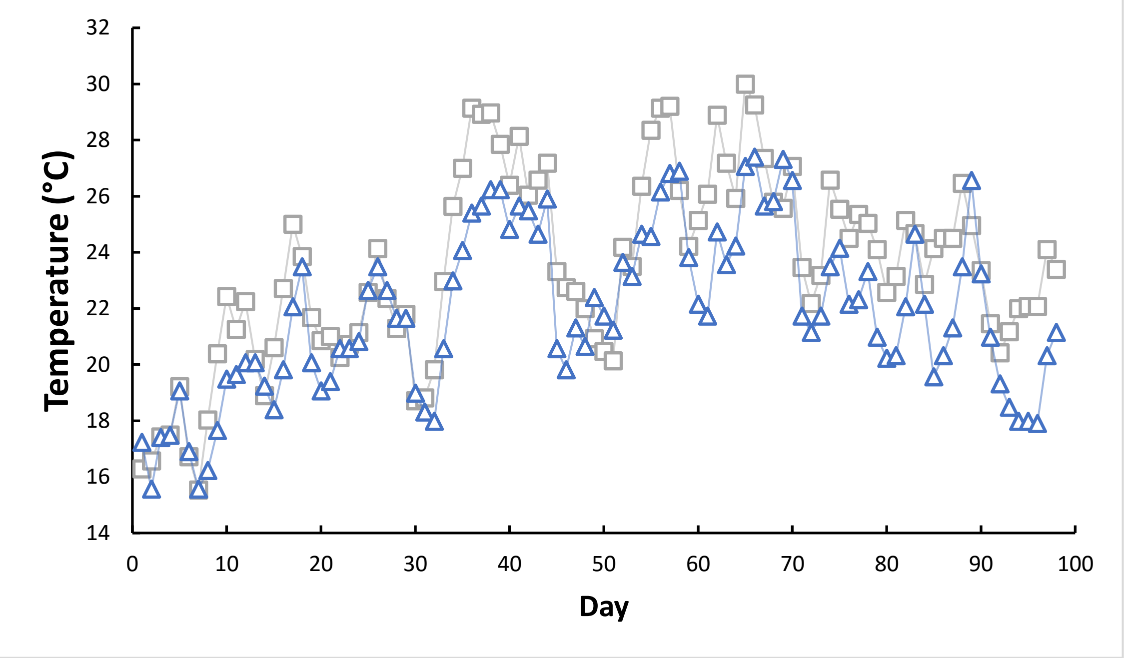


Figure 12. Minimum daily temperatures recorded inside communal nests during the 100 day incubation period. Temperature measurements were recorded from 23rd November 2018 to 28th February 2019. Grey squares show minimums for Morton while blue triangles show minimums for Yengo.

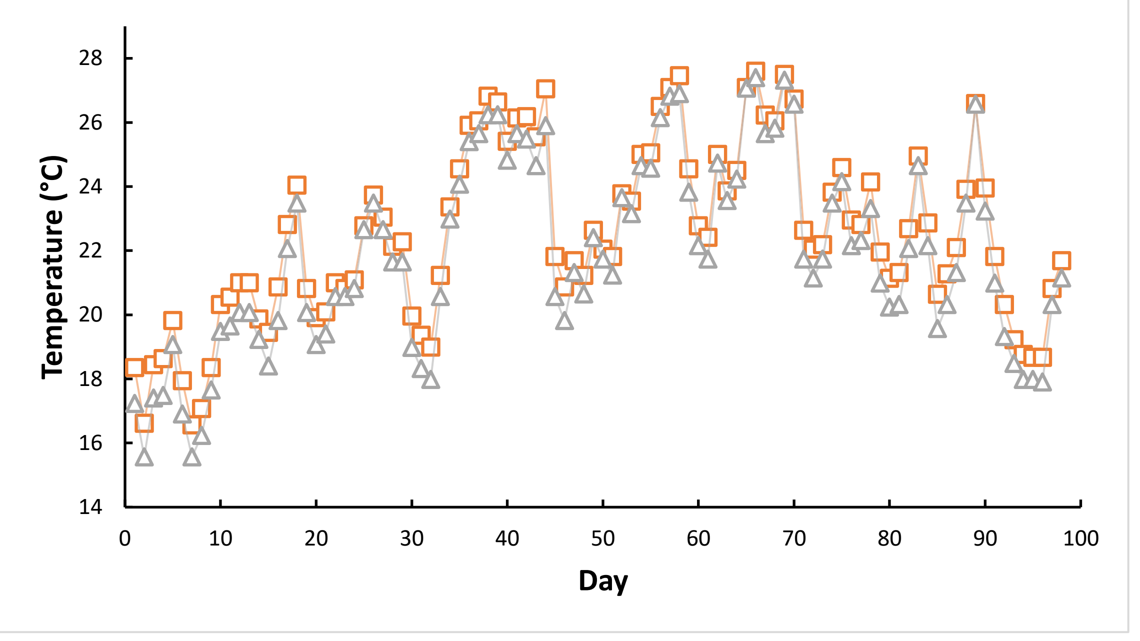


Figure 13. Minimum daily temperatures recorded in Yengo study site inside communal nests and crevices available on the landscape, during the 100 day incubation period. Temperature measurements were recorded from 23rd November 2018 to 28th February 2019. Orange squares show minimums for crevices while grey triangles show minimums for nests.

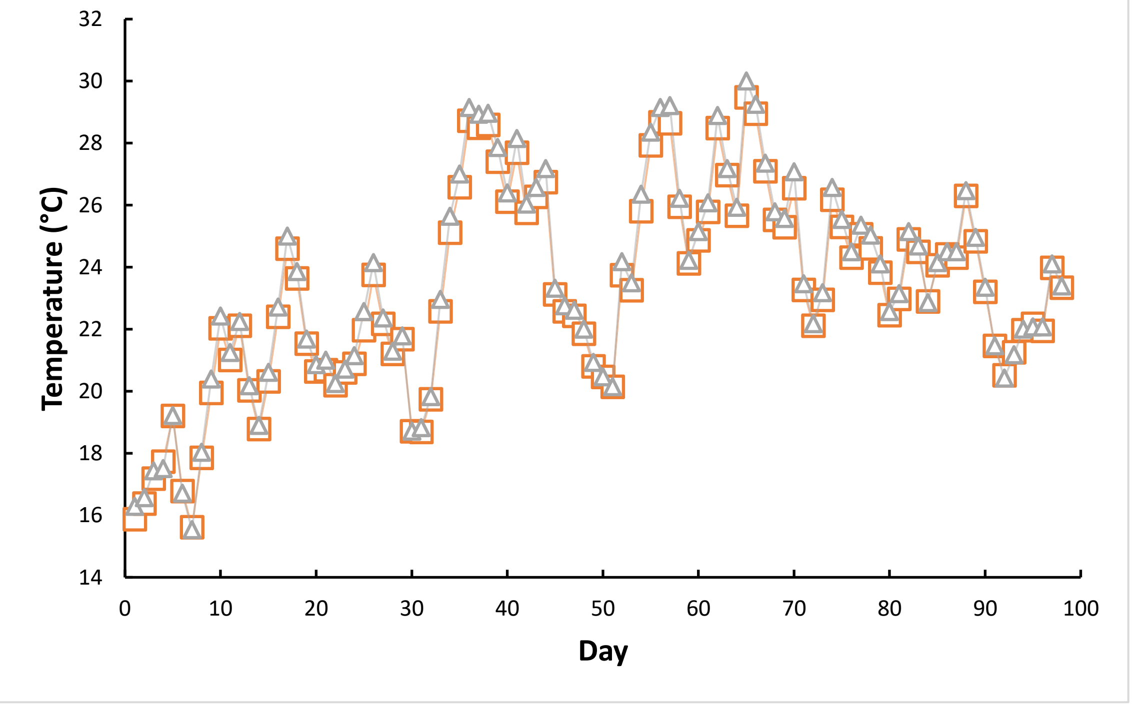


Figure 14. Minimum daily temperatures recorded in Morton study site inside communal nests and crevices available on the landscape, during the 100-day incubation period. Temperature measurements were recorded from 23rd November 2018 to 28th February 2019. Orange squares show minimums for crevices while grey triangles show minimums for nests.

Maximum daily temperatures were significantly different during the summer (see Figure 15) ($F_{(1,97)}$ = 260.4, p = 0.000), and between sites ($F_{(1,58)}$ = 6.516, p = 0.013), but not between types of crevice ($F_{(1,58)}$ = 2.254, p = 0.139), nor for the interaction of both factors ($F_{(1,58)}$ = 0.299, p = 0.587).

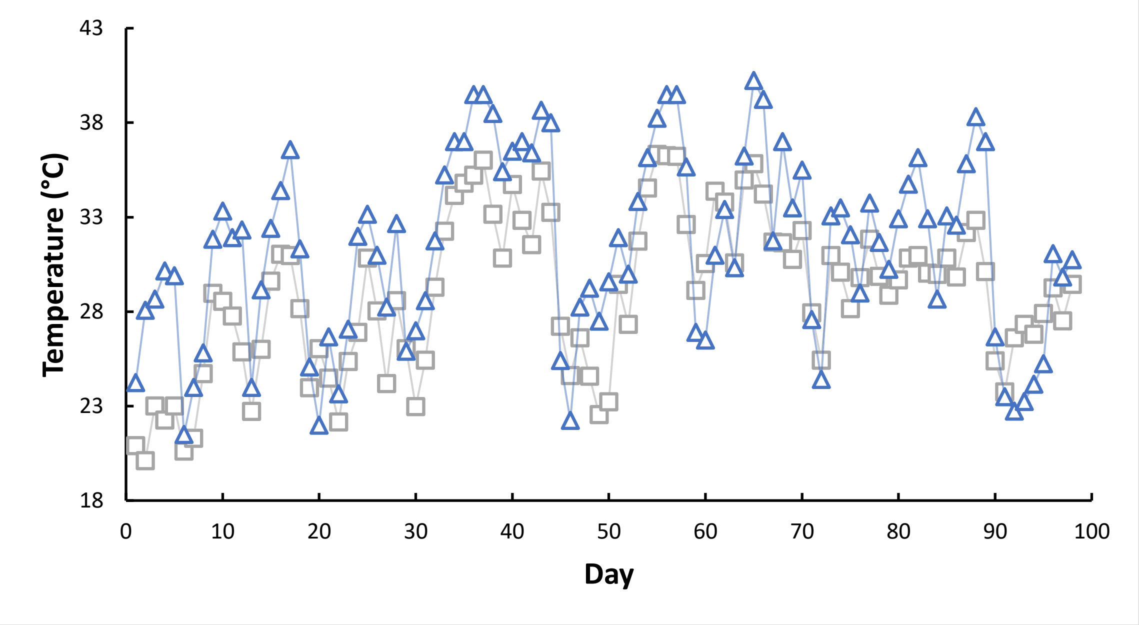


Figure 15. Maximum daily temperatures recorded inside communal nest during the 100-day incubation period. Temperature measurements were recorded from 23rd November 2018 to 28th February 2019. Grey squares show maximums for Morton while blue triangles show maximums for Yengo.

Mean daily temperatures also varied throughout the incubation period ($F_{(1,97)}$ = 738.91, p = 0.000, see Figure 16), but was not statistically different between sites ($F_{(1,58)}$ = 0.011, p = 0.918), types of crevice ($F_{(1,58)}$ = 1.05, p = 0.309), or the interaction of both factors ($F_{(1,58)}$ = 0.05, p = 0.821).

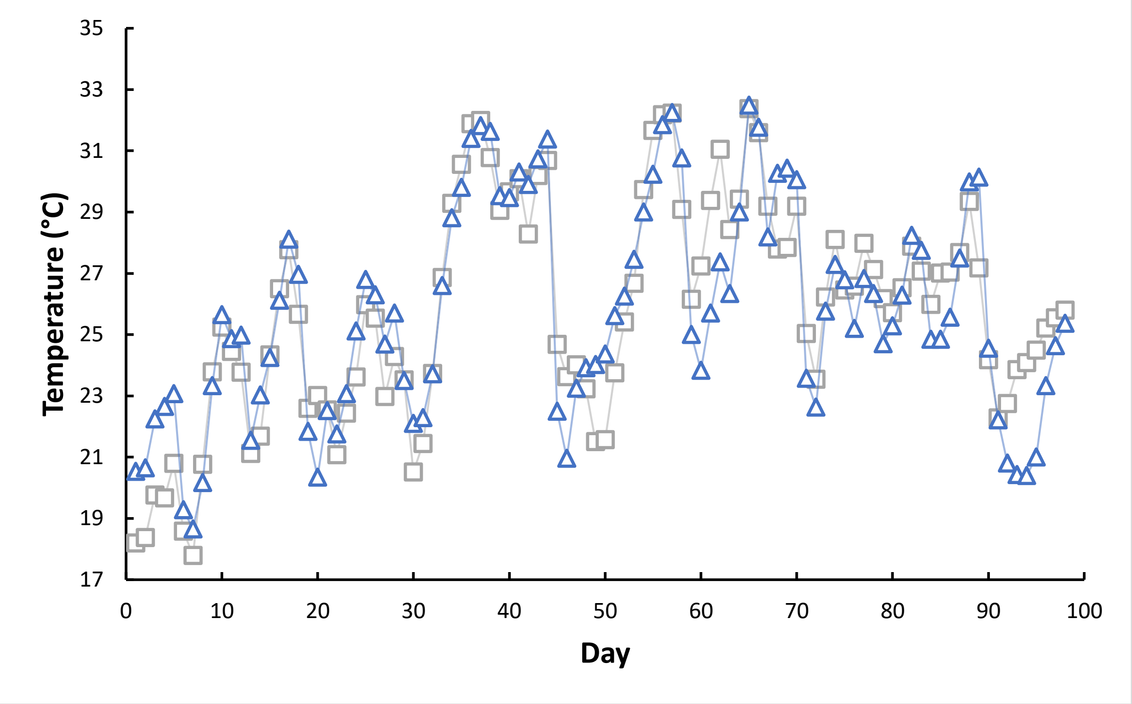


Figure 16. Mean daily temperatures recorded inside communal nests during the 100-day incubation period. Temperature measurements were recorded from 23rd November 2018 to 28th February 2019. Grey squares show means for Morton while blue triangles show means for Yengo.

Both minimum and maximum air temperatures, retrieved from the nearest weather station to the study sites, were positively correlated with temperatures inside nests and crevices. However, Yengo had stronger correlations than Morton both for the minimum and maximum daily temperatures (see Figure 17; Appendix Table 4).

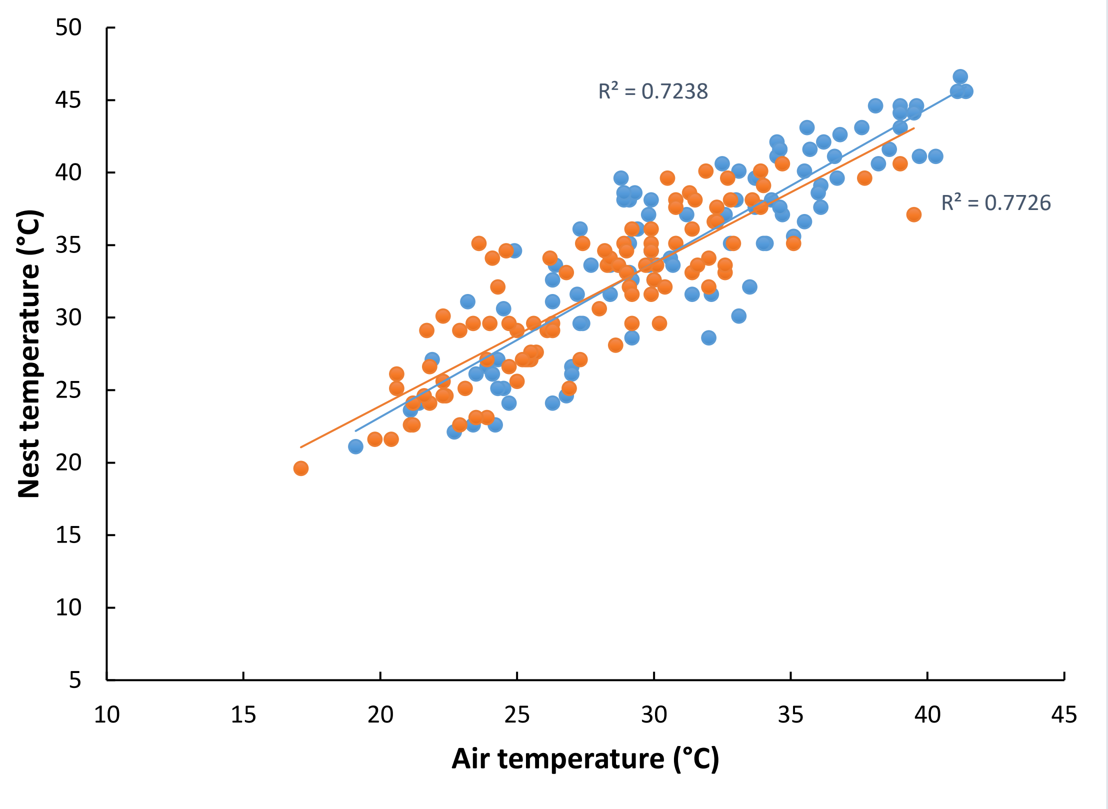


Figure 17. Correlation between maximum daily air temperatures and maximum daily nest temperatures for a nest from Morton (orange) and a nest from Yengo (blue). Air temperatures are from nearest weather stations to each site. Solid orange line indicates line of best fit for Morton, while the blue line shows line of best fit for Yengo.

Some nests were hotter than others and had temperatures which exceeded the species CT_{max} (39.9°C). More than 50% of nests at Yengo, and 13% of nests at Morton experienced at least 1 hour above this temperature during the incubation period (see Figure 18, Figure 19). During this period, the hottest nest in Morton (ns2n1_n_1) and Yengo (prc_1) experienced 16 and 21 days respectively, and a total of 39 and 55 hours, during which nest temperatures exceeded 39.9°C.

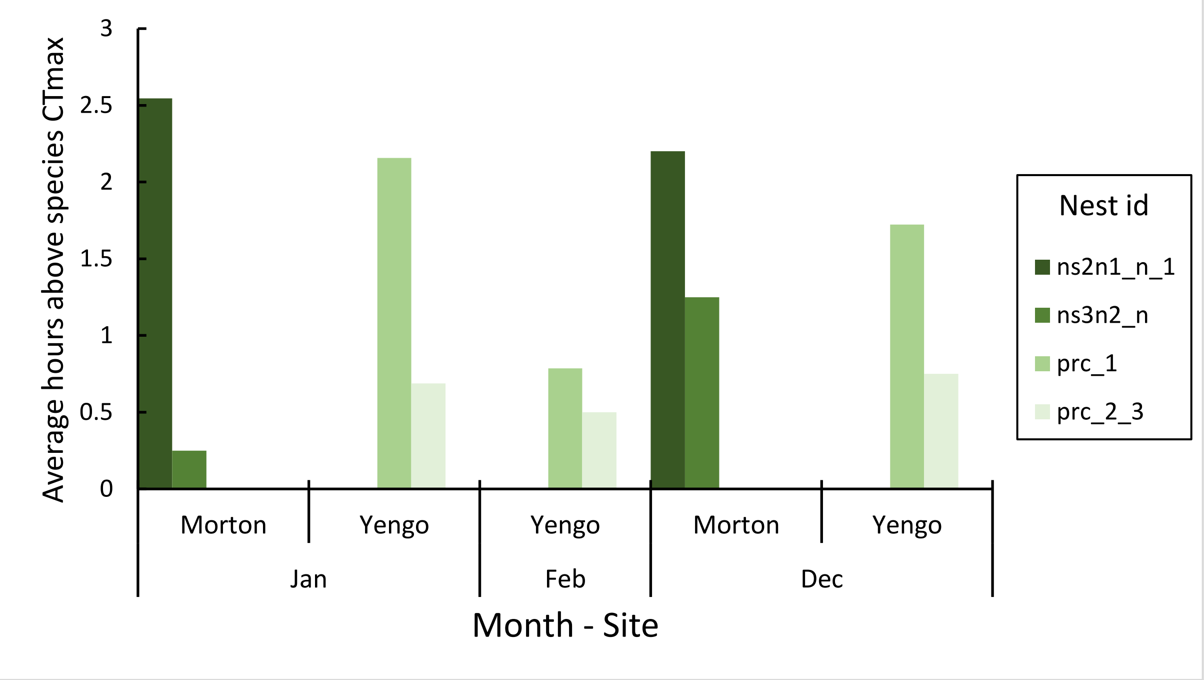


Figure 18. Monthly average of hours per day on which nests had reports of temperatures above species CTmax.

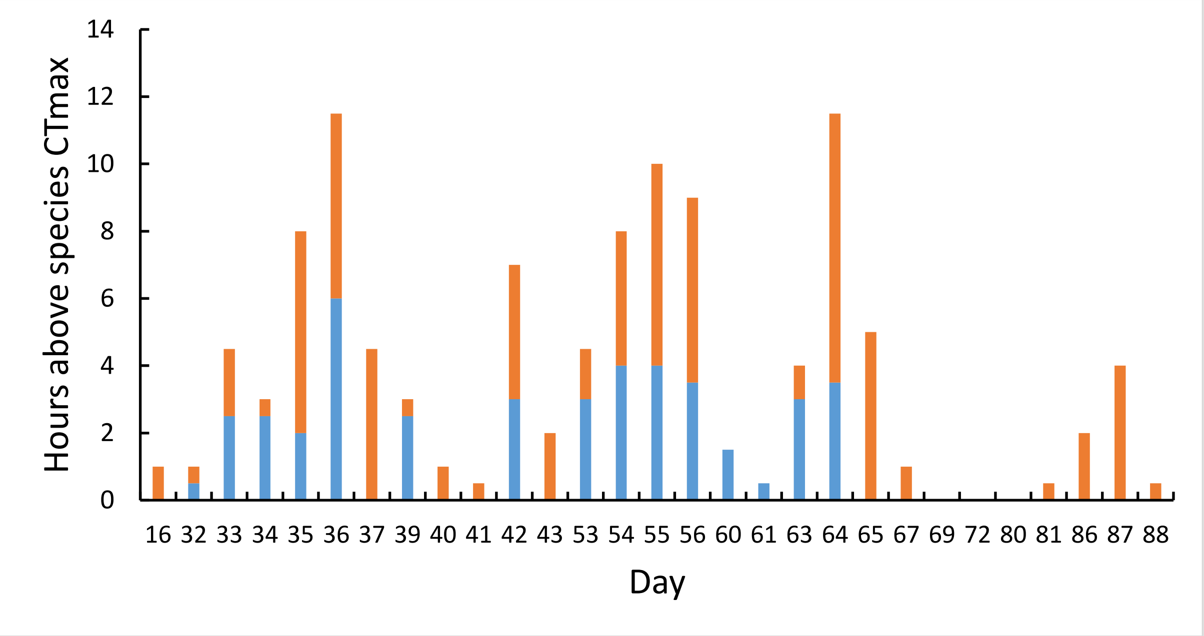


Figure 19. Sum of number of hours during which temperatures inside communal nests exceeded species CT_{max}. Day corresponds to incubation period day. Bars correspond to the sum of hours for all the nests on each site. Orange bars Yengo, blue bars Morton.

2.5. Discussion

In this study, I investigated whether females from a species with a broad latitudinal range modify their nest site choices to compensate for thermal variation. I predicted that females would select nest sites with less canopy cover in the colder southern site, and more canopy cover in the warmer northern site. As predicted, I found that geckos from the southern site (Morton) selected nest sites that were more open, and which received more solar radiation, than nests from the northern site (Yengo). This pattern mirrors the pattern of maternal oviposition site choice displayed by the water dragon (Doody, Guarino, Georges, *et al.*, 2006), and some turtles including the snapping turtle (*Chelydra serpentina*; Ewert, Lang, & Nelson, 2005); and the painted turtle (*Chrysemys picta*, Refsnider, Milne-Zelman, Warner, & Janzen, 2014). I also predicted that if females aim to maximise offspring fitness, then mean and maximum nest temperatures would be similar across latitudes. My results partially supported this prediction; mean temperatures of communal nests from Morton and Yengo were virtually identical (Figure 16), but unexpectedly, maximum nest temperatures were higher at Yengo than at Morton (Figure 15).

This difference in maximum nest temperatures can be explained by geographic differences in air temperatures and structural features of nests. I found strong significant positive correlations between maximum daily air temperatures and nest temperatures at both locations, but maximum air temperatures were higher at Yengo than at Morton (Figure 17). The finding that nest temperatures are tightly linked to air temperatures supports the results of a previous study (Dayananda *et al.*, 2016). Unexpectedly, minimum nest temperatures were lower at Yengo than

Morton, suggesting that nests in Morton had physical attributes that provided more buffering from thermal extremes. When I examined the physical attributes of nests, I found nests at Morton had greater thickness of rock above them (mean = 69.6 cm) than at Yengo (mean = 50.6 cm). Previous studies have shown that rock thickness influences temperatures of crevices under rocks; if solar radiation loads are similar, thin rocks will attain higher temperatures than thick rocks (Huey *et al.*, 1989; Webb & Shine, 1998; Croak *et al.*, 2008). Hence, by selecting more open nest sites, and nest sites with greater rock thickness, females at Morton provided nest sites that were buffered from high and low temperatures.

Interestingly, at small spatial scales (20 m), I found no evidence that females were selecting nest crevices based on their structural or thermal regimes. That is, there were vacant, potentially suitable nest sites available to females near currently used nest crevices. A previous study found that at larger spatial scales, female velvet geckos seldom lay eggs inside crevices under rocks or boulders, even though such features are abundant in the landscape. Females avoid ovipositing in these sites because temperatures in crevices under these structures are too hot for embryos to tolerate (Pike, Webb and Shine, 2010). Relative humidity was also more stable in nesting crevices than in crevices under boulders or rocks. Thus, at larger spatial scales, females may choose crevices on rock walls because they do not experience lethally high temperatures and provide humid environments that prevent eggs from desiccating.

Over the incubation period, I found that nest temperatures fluctuated in response to local weather conditions, as has been reported for lizards that lay eggs in soil nests. However, during summer, 50% of Yengo nests, and 13.3% of Morton nests, experienced temperatures > 39.9°C for 1 hour or more (see Figure 18, Figure 19). The hottest nests in Morton and Yengo reported more than 39 and 55.5 hours respectively, above 39.9°C. These nests experienced extreme temperatures for prolonged hours. For example, prc_1, registered 5.5 continuous hours above 39°C with a maximum temperature of 45.6°C on the 17th and 18th of January 2019. This coincided with the hottest January day registered for Richmond RAAF base, when ambient air temperatures reached 41.1°C (17th January). While embryos may survive short exposures to high temperatures, longer exposures may affect embryo survival. Previous studies on the velvet gecko found that eggs incubated at 27.0°C (range 14–37°C) had lower hatching success (54.5%) than eggs incubated at 23.2°C,(range 10–33°C, 86.4%) (Dayananda and Webb, 2017). Following release to the wild, hatchlings from the 27.0°C treatment had higher mortality rates (99%), than hatchlings from the 23.2°C treatment (11%) (Dayananda *et al.*, 2016). That study did not include incubation temperatures greater than the geckos CT_{max}, so the temperatures that I recorded in nests may lead to higher mortality of embryos. For example, an experimental study on the lizard *Sceloporus tristichus* found that embryo survival dramatically declined in eggs that were exposed to several hours of high temperatures (40, 41 or 43°C) over a 7 day period (Telemeco *et al.*, 2017). Future experimental studies, similar to those carried out by Telemeco et al. 2017 are necessary to elucidate whether brief, and more prolonged exposures, to high temperatures affect embryo survival or offspring phenotypes in my study species.

My data also allows me to examine hypotheses for the evolution of communal nesting in squamates. The simplest explanation for this behaviour is that females choose to lay communally because appropriate nest sites are rare in the environment. I found no difference in the physical or thermal characteristics of unused crevices and nesting crevices. Hence, my data does not support this hypothesis. In fact, unused crevices were common within a 20 m radius of nesting crevices. Plausibly, females may lay eggs communally because it reduces the chances of desiccation (Radder and Shine, 2007) and may provide additional benefits to offspring post-hatching. For example, studies on the Australian freshwater turtle (*Emydura macquarii*) showed that less-developed embryos increased both metabolic and heart rates to synchronise hatching with more developed eggs from the same clutch (McGlashan, Spencer and Old, 2012). It was also recently reported that developing embryos from the water snake (*Natrix maura*), use heart beats from eggs within the same clutch, and in physical contact, to synchronise development and hatching (Aubret *et al.*, 2016). This could ultimately represent an advantage, as hatching synchrony could increase predator swamping and kin recognition. Velvet gecko hatchlings share rocks during the first few weeks of life, with 3 or 4 usually found together under the same rock (Webb, unpublished data), which suggest some mechanism underlying hatching synchrony. Irrespective of the mechanisms driving communal egg laying in my study species, this behaviour renders populations vulnerable to prolonged heatwaves. That is, during heatwaves, a high proportion of eggs within a local population may experience lethally high temperatures. Interestingly, long-term data suggests that female velvet geckos show strong philopatry to nest sites. Whether females can determine that eggs failed to hatch in a previous summer is not known. Future studies could examine whether females can distinguish between hatched and unhatched eggs. If females cannot adjust their nest-site selection for future reproduction events, they may be caught in an ecological trap that renders them vulnerable to rising temperatures (Kolbe and Janzen, 2002).

In conclusion, I found strong geographic variation in the physical and thermal characteristics of nest sites of velvet geckos. These findings suggest that females can adjust nesting decisions to suit local environments. However, because temperatures of crevices are strongly influenced by air temperatures, nests in the northern population are at higher risk of heatwaves than nests in the southern population. Future research should address whether exposure to high temperature compromises hatching success or hatchling traits in this population.

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Appendix

Table 4. Correlation between air temperatures (retrieved from nearest station to study sites) and measured nests and crevices temperatures.

Site	Thermochron_ID	Crevice type	Maximum temperature
			Pearson correlation
Morton	camp_c_1	crevice	.732**
Morton	camp_c_2	crevice	.487**
Morton	camp_c_3	crevice	.672**
Morton	climb_c_1	crevice	.867**
Morton	climb_c_2	crevice	.639**
Morton	climb_c_3	crevice	.736**
Morton	climb_c_4	crevice	.810**
Morton	n395_c_1	crevice	.733**
Morton	n395_c_2	crevice	.837**
Morton	n395_c_3	crevice	.697**
Morton	ner1_c_1	crevice	.733**
Morton	ner1_c_2	crevice	.788**
Morton	ner1_c_3	crevice	.772**
Morton	nngps155_c_2	crevice	.653**
Morton	ns2n1_c_1	crevice	.850**
Morton	ns2n1_c_2	crevice	.810**
Morton	ns2n1_c_3	crevice	.611**
Morton	ns2n1_c_4	crevice	.678**
Morton	ns3n1_c_1	crevice	.605**
Morton	ns3n1_c_2	crevice	.757**
Morton	ns3n2_c_3	crevice	.700**
Morton	ns3n3_c_1	crevice	.759**
Morton	ns3n3_c_2	crevice	.765**
Morton	ns3n3_c_3	crevice	.632**
Morton	site4n3_c_2	crevice	.681**
Morton	site4n3_c_3	crevice	.779**
Morton	yar1_c_1	crevice	.712**
Morton	yar1_c_3	crevice	.766**
Morton	yarramun_c_1	crevice	.840**
Morton	yarramun_c_2	crevice	.778**
Morton	yarramun_c_3	crevice	.605**
Morton	climb_1	nest	.737**
Morton	climb_2	nest	.811**
Morton	climb_3	nest	.750**
Morton	climb_4	nest	.709**
Morton	n395_c_4	nest	.659**

Morton	nngps155_1	nest	.662**
Morton	ns2n1_n_1	nest	.799**
Morton	ns2n1_n_2	nest	.657**
Morton	ns3n1_c_3	nest	.746**
Morton	ns3n2_n	nest	.851**
Morton	ns3n3_n	nest	.693**
Morton	site4n3_c_1	nest	.761**
Morton	site4n3_n	nest	.702**
Morton	yar1_n_p5	nest	.768**
Yengo	prc_1_1	crevice	.858**
Yengo	prc_1_w	crevice	.730**
Yengo	prc_1_x	crevice	.855**
Yengo	prc_2_2	crevice	.831**
Yengo	prc_3_1	crevice	.872**
Yengo	prc_3_2	crevice	.861**
Yengo	prc_3_3	crevice	.783**
Yengo	prc_4_3	crevice	.859**
Yengo	prc_5_3	crevice	.793**
Yengo	prc_6_2	crevice	.889**
Yengo	prc_6_3	crevice	.768**
Yengo	prc_1	nest	.879**
Yengo	prc_2_3	nest	.834**
Yengo	prc_4	nest	.866**
Yengo	prc_4_2	nest	.877**
Yengo	prc_5_1	nest	.842**
Yengo	prc_6_1	nest	.878**

****. Correlation is significant at the 0.01 level (2-tailed).**

Chapter 3. Geographic range and shifts under climate change for the Australian endemic velvet gecko (*Amalosia lesueurii*).

3.1. Abstract

Reptiles are susceptible to changes in climate because their physiology and behaviour is strongly influenced by temperature. However, reptiles may adapt to shifts in climate by migrating to new areas. In the present study, I investigated the distribution under current and future climatic conditions of the velvet gecko *Amalosia lesueurii*. I modelled the species distribution under current climate using the algorithm MaxEnt. I used 1019 occurrences, the Australian Current Climate bioclimatic variables, and the altitude to define the environmental space of the species, and defined the calibration area based on the Australian bioregions. After constructing the species distribution model, I projected the shifts in range to the years of 2025, 2045, 2065, and 2085 under four different emission scenarios from the Intergovernmental Panel on Climate Change (IPCC). My results show high probabilities of occurrence across the Sydney Basin, the New England Tablelands, and surprisingly on the southern part of New South Wales (NSW) North Coast. Under future climates, the species will suffer range contractions that exceed range expansions in all of the projected years and under every emission scenario. The greatest losses will occur in the Sydney Basin region and New England Tablelands. Loss of the velvet gecko from the Sydney region would have serious consequences for the persistence of a vulnerable predator (broad-headed snake, *Hoplocephalus bungaroides*) which relies on geckos as a food source. My study highlights the how climate change can affect a widespread

Australian endemic gecko species and highlights the importance of proactive management to conserve future populations.

3.2. Introduction

Global climate change poses a great challenge for biodiversity on all its levels. According to recent modelling predictions, if temperatures continue to rise, and the observed global mean surface temperature (GMST) exceeds the 1.5 °C limit that the Paris agreement set, the effects on all life on earth will be catastrophic (IPCC, 2018; Warren *et al.*, 2018). For example, a recent paper suggested that of 100,000 species for which there was data, 49% of the insects, 44% of plants, and 26% of vertebrates would lose more than 50% of their projected geographic ranges by 2100 if the temperature trend continues and GMST reach 3.2°C above pre-industrial levels (Warren *et al.*, 2018). Among vertebrates, reptiles are particularly at risk from temperature changes as their physiology and behaviour is tightly linked to environmental temperatures. Global estimates based on climatic modelling have suggested that at least 40% of reptile species will lose more than 90% of their range by 2050 (Warren *et al.*, 2018). Understanding how climate change will affect individual species is crucial for managing and conserving biodiversity (Lovejoy and Hannah, 2018).

The natural distributional range encompasses the physical space in which species currently occur. If organisms respond to rising temperatures by tracking optimal environmental conditions, we can expect shifts in distributional ranges. However, for some species, such shifts can be restricted by anthropogenic habitat fragmentation and/or poor dispersal abilities of the organisms (Araújo and New, 2007). Usually the process through which species respond to increasing temperatures is via expansion or dispersion on the cold-edge (moving to higher latitudes, towards the poles) and contractions or population extinctions on the warm-edge of the species (lower latitudes, towards the tropics) (Wiens, 2016; Warren *et al.*, 2018; Figure 2).

Species distribution modelling (SDM) is a well-known method that infers the range of a species based on the Hutchinsonian environmental hyperspace of species or the realized ecological niche. These models use occurrence or abundance data of species to generate environmental variables that predict the geographical range where those variables are present, and thus the realized ecological niche of the species (Kearney, Wintle and Porter, 2010). There are two main approaches for estimating geographic ranges: the correlative (or statistical) approach, and the mechanistic (or physiological) approach (Kearney and Porter, 2009). These models serve two main purposes, interpolation or extrapolation. For interpolation, training data is used to predict novel areas both within the same range of the sampled environments and the sampling time frame (Elith and Leathwick, 2009). Interpolation can be used to analyse species distributions on global scales, visualizing species scarcity across a defined region, and identifying new suitable areas for uncommon species without major theoretical risks (Guisan and Thuiller, 2005). On the other hand, extrapolation or forecasting is used to predict occurrence outside the sampled geographic space and/or over different time frames (i.e. under past or future environmental conditions: Araújo and New, 2007; Elith and Leathwick, 2009).

Correlative SDMs are more commonly used because they use easily available data and have been proven to predict species ranges with a good precision (Elith and Leathwick, 2009). Species distribution models are a powerful tool that are useful for identifying areas that should be prioritised for conservation of endangered species or endangered ecosystems (Guisan *et al.*, 2013). SDMs can also help to evaluate the potential for invasive species to settle in new habitats (Václavík and Meentemeyer, 2012) and determine the potential spread of vectors of infections and diseases that affect public health and ecosystems (Campbell *et al.*, 2015). Last, but not least, SDMs allow us to predict the effects of climatic changes on biodiversity (Cabrelli and Hughes, 2015; Levy *et al.*, 2015; Freeman, Sunnarborg and Peterson, 2019).

In the present study I used correlative models to investigate how a widely distributed reptile, the velvet gecko *Amalosia lesueurii* might respond to increasing temperatures. This abundant and widely distributed lizard occurs on the east coast of Australia from south-eastern Queensland (QLD) to south-eastern NSW (Cogger, 2014). This rock dwelling lizard is long-lived, has low reproductive output, and it occurs in one of Australia's most fragmented landscapes. Genetic studies have revealed that there is low gene flow between populations, even in relatively intact areas (Dubey *et al.*, 2012). Velvet geckos lay eggs in communal nests, and nest temperatures are highly correlated with air temperatures (Chapter 2**;** Dayananda *et al.*, 2016). Previous incubation studies have found that exposure of eggs to higher temperatures reduces hatching success, and produces hatchlings that have lower survival (Dayananda *et al.*, 2016; Telemeco *et al.*, 2017)**.** Thus, this gecko species possesses a suite of life history and behavioural traits may render populations vulnerable to extinction, so it is important to understand how the species distribution may change under future climates. To investigate how the species range may change in future, I modelled the species distribution with MaxEnt algorithm and projected the shifts in range to different climate change scenarios.

3.3. Materials and methods

3.3.1. Study species

The Australian endemic Lesueur's velvet gecko (*Amalosia lesueurii*) is a nocturnal lizard that inhabits caves and crevices in rocky outcrops and ridges along the east coast of Australia. It is an extensively studied, and abundant species with a large geographic distribution that extends from south-eastern QLD to south-eastern NSW (Cogger, 2014). According to recent phylogeographic studies, the species lies within the *Amalosia* clade along with *A. obscura, A. rhombifer,* and *A. jacovae* (Couper, Keim, & Hoskin, 2007; Oliver *et al.*, 2012). The latter species shares its geographic range with *A. lesueurii* in south-eastern QLD, however, they differ in morphological characters such as the dorsal pattern, the 1st and 2nd supra-labial scales, and the webbing between the 3rd and 4th toes (Couper, Keim and Hoskin, 2007).

Female velvet geckos lay eggs inside communal nesting crevices, and select nest sites based on specific structural and physical features (e.g. Chapter 2) (Pike, Webb and Shine, 2010; Pike, Webb and Andrews, 2011). Previous studies have suggested that nest temperatures are strongly influenced by ambient air temperatures (Dayananda *et al.,* 2016; Chapter 2). Additionally, laboratory incubation experiments have found that eggs incubated under current thermal conditions (mean = 23.2°C, range = 10 – 33°C) produced larger hatchlings, which had higher survival than hatchlings from future thermal regimes (mean = 27°C, range = 14 – 37°C) (Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017). These results highlight that the early life stages of this species' are sensitive to temperature, which makes the species a good candidate for exploring how future temperatures might affect populations.

3.3.2. Occurrences records

I retrieved 3028 records for the Lesueur's velvet gecko (*Amalosia lesueurii*) from the Atlas of Living Australia (ALA), and 3040 from the Global Biodiversity Information Facility (GBIF). I unified the records and filtered duplicates, and excluded data points with poor precision (> 100m) or with insufficient data. I also removed outliers that were clearly outside of the species reported range (i.e. records in South Australia, the Northern Territory, and far north QLD; (Cogger, 2014). I also excluded records prior to 1970 to avoid inconsistencies with climate data (Chapman, 2005). After filtering the data, I randomly thinned the records with 1 km of buffer between occurrences, leaving a dataset with 1019 points of occurrence (Figure 20).

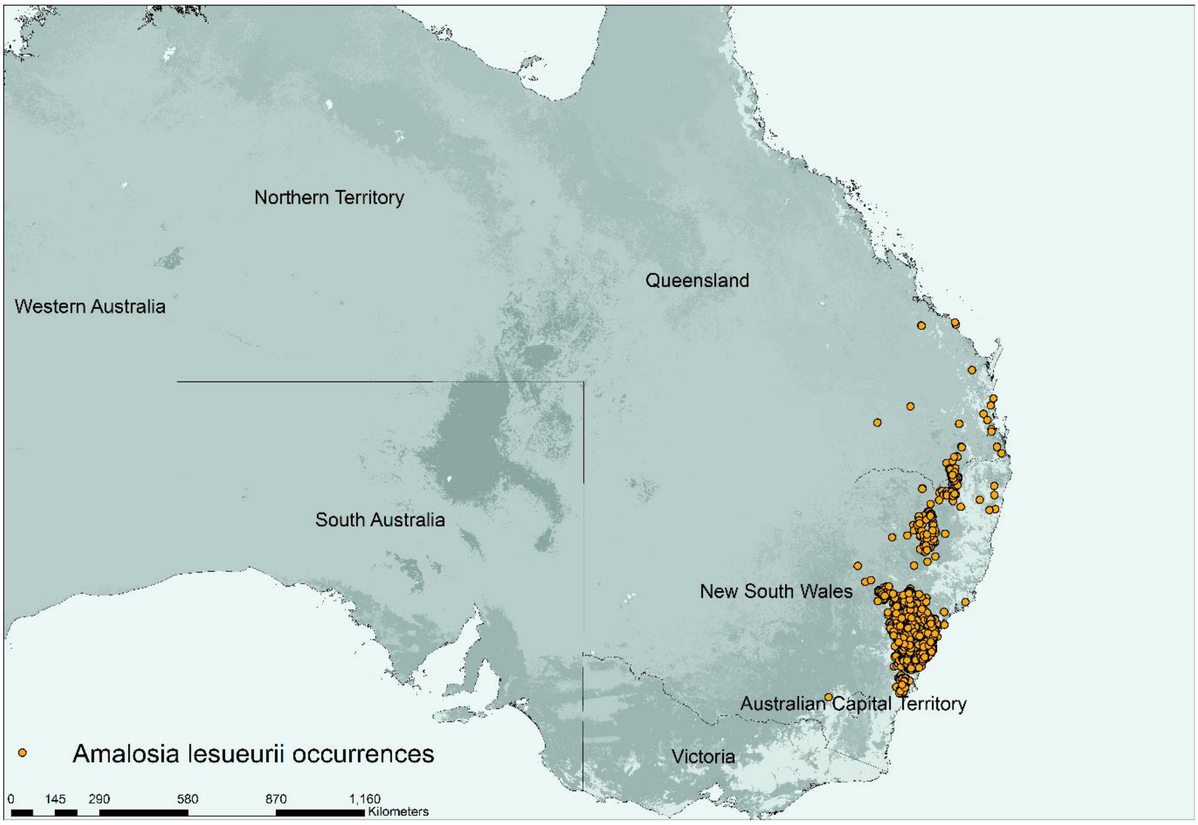


Figure 20. Occurrences for *Amalosia lesueurii* after processing.

3.3.3. Species distribution model

To define the species environmental space I used the 19 bioclimatic variables from Australia, current climate (1976-2005), 30 arcsec (~1 km) spatial resolution (Vanderwal, 2012). Additionally, for a topographic variable I used the altitude from WorldClim at 2.5 archmin (~5 km) (Fick and Hijmans, 2017). I tested for correlations between all variables and eliminated a variable from each pair where the Pearson correlation coefficients were > 0.8 (as in Freeman *et al.*, 2019). I also prioritised variables according to the species ecological traits. For instance, high temperatures during the incubation period can negatively affect hatchlings (Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017). I prioritised B05 - Max Temperature of the Warmest Month over other temperature variables. I then ran the algorithms on 11 variables (see Appendix Table 5).

The calibration region (also called M) is the geographic space that is accessible to a certain species in a given time, and defining it is a crucial step for ecological niche modelling (Bar*ve et al.*, 2011; Freeman, Sunnarborg and Peterson, 2019). For the present study, I defined M based on the Interim Biogeographic Regionalisation for Australia (IBRA) version 7.0. I selected the bioregions with the highest occurrences for the species with a buffer of one bioregion outside these (Peterson *et al.*, 2011; Freeman, Sunnarborg and Peterson, 2019). After delimiting M, I masked to its extent all the environmental variables in ArcGIS 10.6.1. For projections in future climatic scenarios, I used the Australian state borders and included Victoria, South Australia, Australian Capital Territory, NSW, QLD and the Northern Territory.

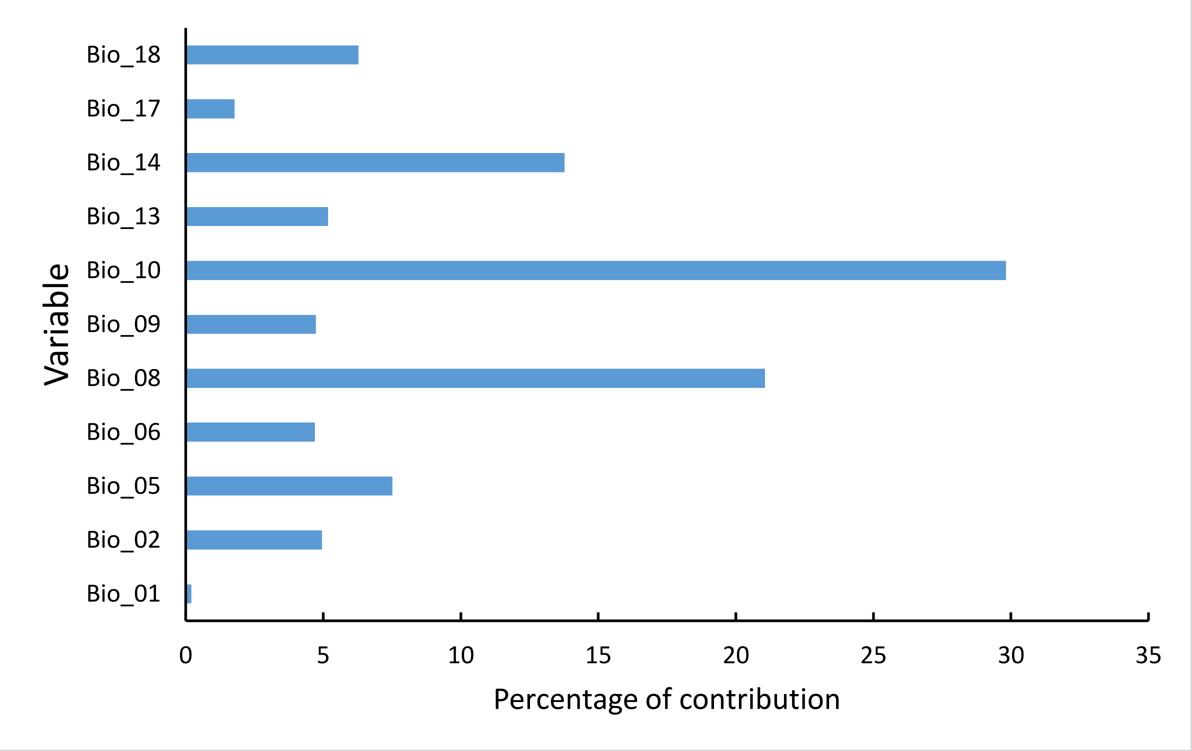
To model the species distribution, I used Maxent algorithm (version 3.3.3k) (Phillips, Anderson and Schapire, 2006). First, I split the occurrence data into 70% and 30% for calibration and evaluation respectively (Freeman, Sunnarborg and Peterson, 2019). The partitioning method I used was the block method as it has been proven to perform better for studies involving climate change effects (Wenger and Olden, 2012). Next, I ran a series of combinations of feature classes and regularization multiplier values of Maxent to find the optimal model complexity (Muscarella *et al.*, 2014; Cobos *et al.*, 2019). I ran 30 possible different combinations of Linear (L), quadratic (Q), product (P), hinge (H) and threshold (T), feature classes, and 16 regularization multipliers (0.1, 0.2…1, 2, 4, 5, 6, 8 and 10) on the ENMeval package for R (Muscarella *et al.*, 2014), using a code generated by Barrios & Cuervo-Robayo (2017). Having a big and diverse set of candidate models is optimal for selecting a model that best explain the species occurrence (Cobos *et al*., 2019; Freeman, Sunnarborg and Peterson, 2019).

I used the Akaike Information Criterion (AIC, Hurvich and Tsai, 1993) and the area under the curve (AUC) to evaluate the best candidate model. I also examined performance on training presence using a 5% threshold evaluating omission (Peterson *et al.*, 2011).

Having found the optimal model, I ran it again on the Biodiversity and Climate Change Virtual Laboratory (BCCVL), an online application that simplifies the process of modelling distributions and climate change impacts (Hallgren *et al.*, 2016). To determine whether the species was predicted in forested areas I projected the predicted distribution over The MODIS Land Cover Type Product (MCD12Q1), using only the classes with tree cover > 60% (classes 1-6; Sulla-Menashe & Friedl, 2019). To describe climate change effects on the species' range, I used four IPCC representative concentration pathways (RCP 2.6, 4.5, 6.0, 8.5) emissions scenarios based on CSIRO-Mark 30 global circulation model (GCM), 30 arcsec (~1 km), for the years 2025, 2045, 2065, and 2085, maximizing sensitivity (TPR) and specificity (TNR) with a threshold of 0.1. These analyses were also run on BCCVL. Then, I used ArcGis for analysing range contractions and expansions on the species with a probability of occurrence threshold of 0.5 (Freeman, Sunnarborg and Peterson, 2019).

3.4. Results

I selected 11 bioclimatic variables after the correlation test (Appendix Table 5). I assessed a total of 480 candidate models resulting from the feature classes and the regularization multipliers (see Appendix Table 6). The best model chosen after the analyses had for settings LHP as feature classes and 1 as regularization multiplier and met the ≤ 5% omission criteria. Based on the percentage of contribution, the most important variables for defining the environmental space of the species were the mean temperature of the warmest quarter, the mean temperature of the wettest quarter, and the precipitation of the driest month (Figure **21**).



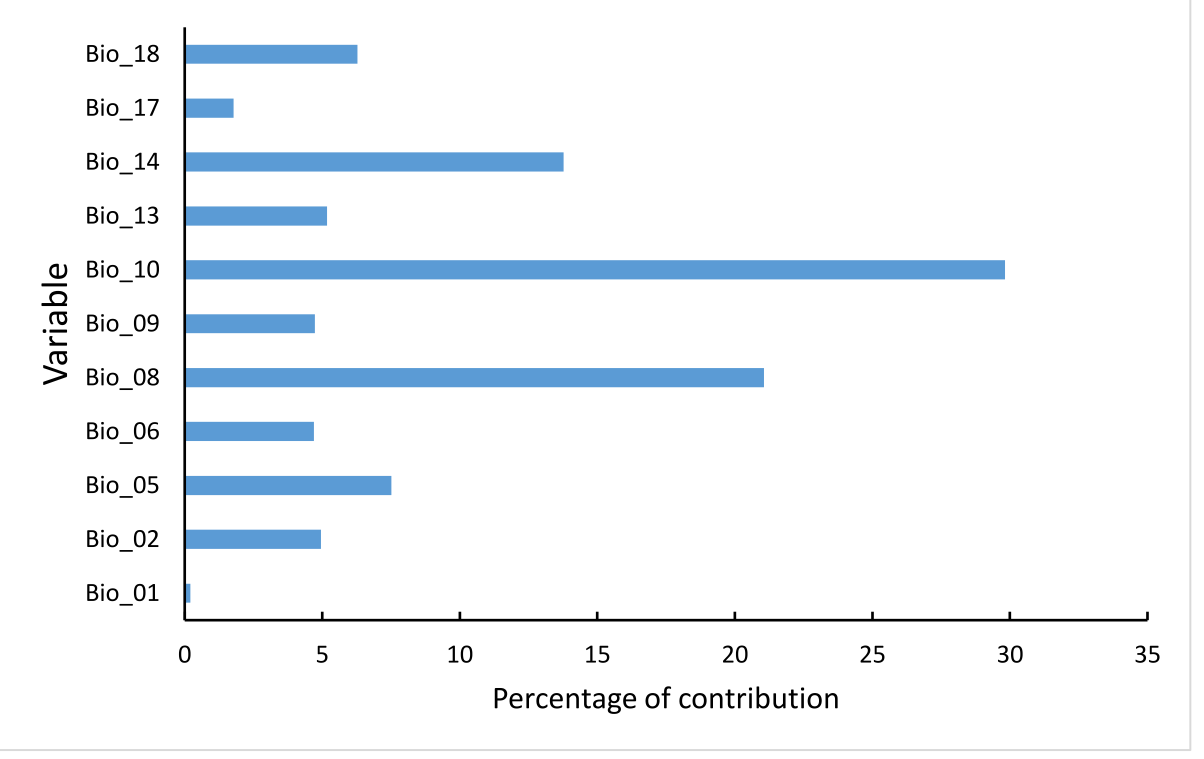


Figure 21. Percentage of contribution of the different bioclimatic variables to the selected optimal model.

Modelling revealed that velvet geckos have a broad potential current distribution with respect to climate (Figure 22). The predicted distribution provided a reasonably good match with the known occurrences for the species, with the highest concentration of predicted presence around the Sydney region, New England Tablelands, and south coast of NSW. However, although the species is predicted to occur on the NSW mid-north coast and south-eastern highlands, there are currently no known records in those regions (Figure 22). A plot of the predicted current distribution overlaid with forest cover showed that large portions of the species range occur in areas that have undergone significant forest loss and fragmentation (Figure 23).

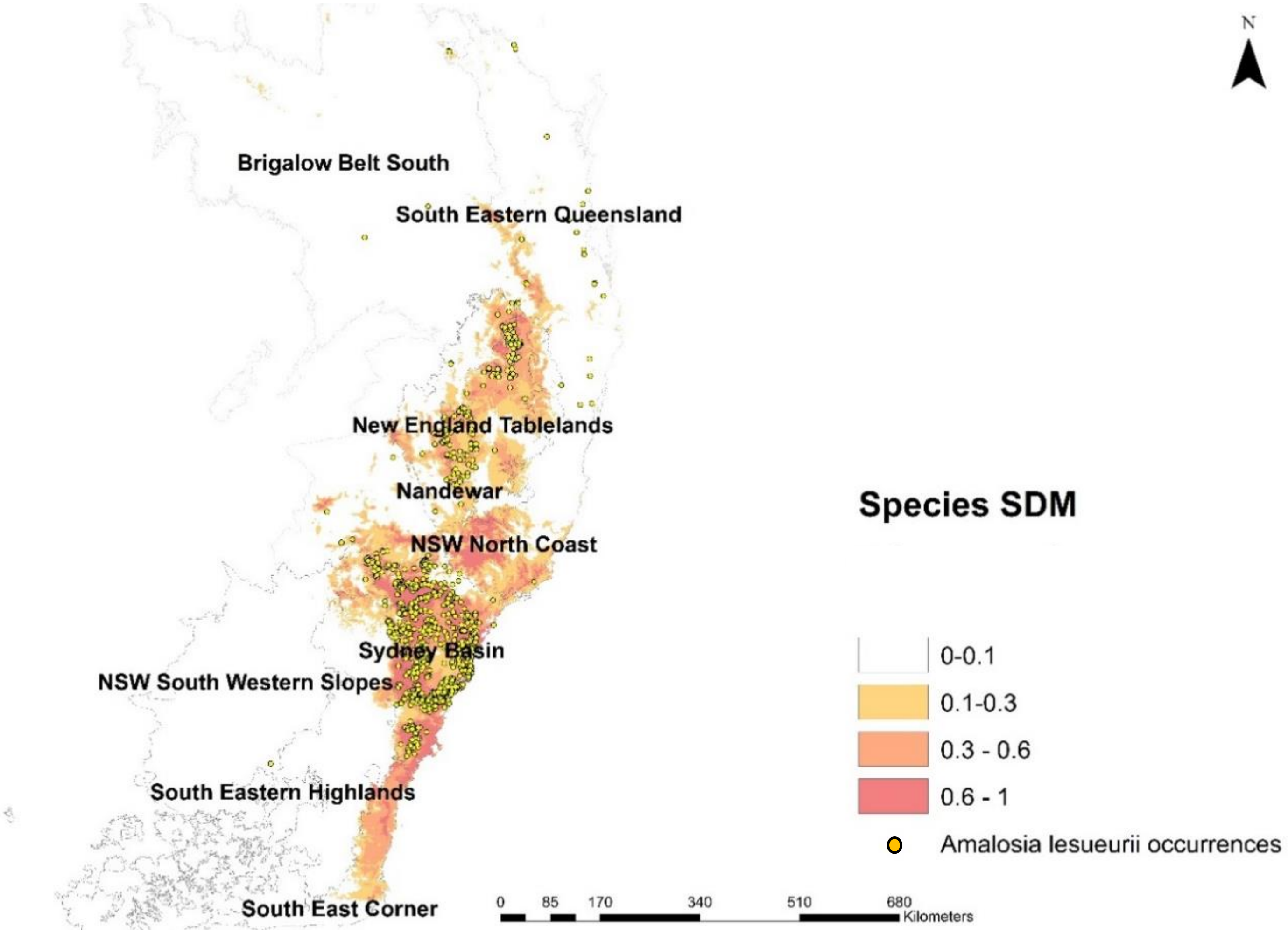


Figure 22. Predictions of the distribution of the velvet gecko (*Amalosia lesueurii*) for current climatic conditions using Maxent.

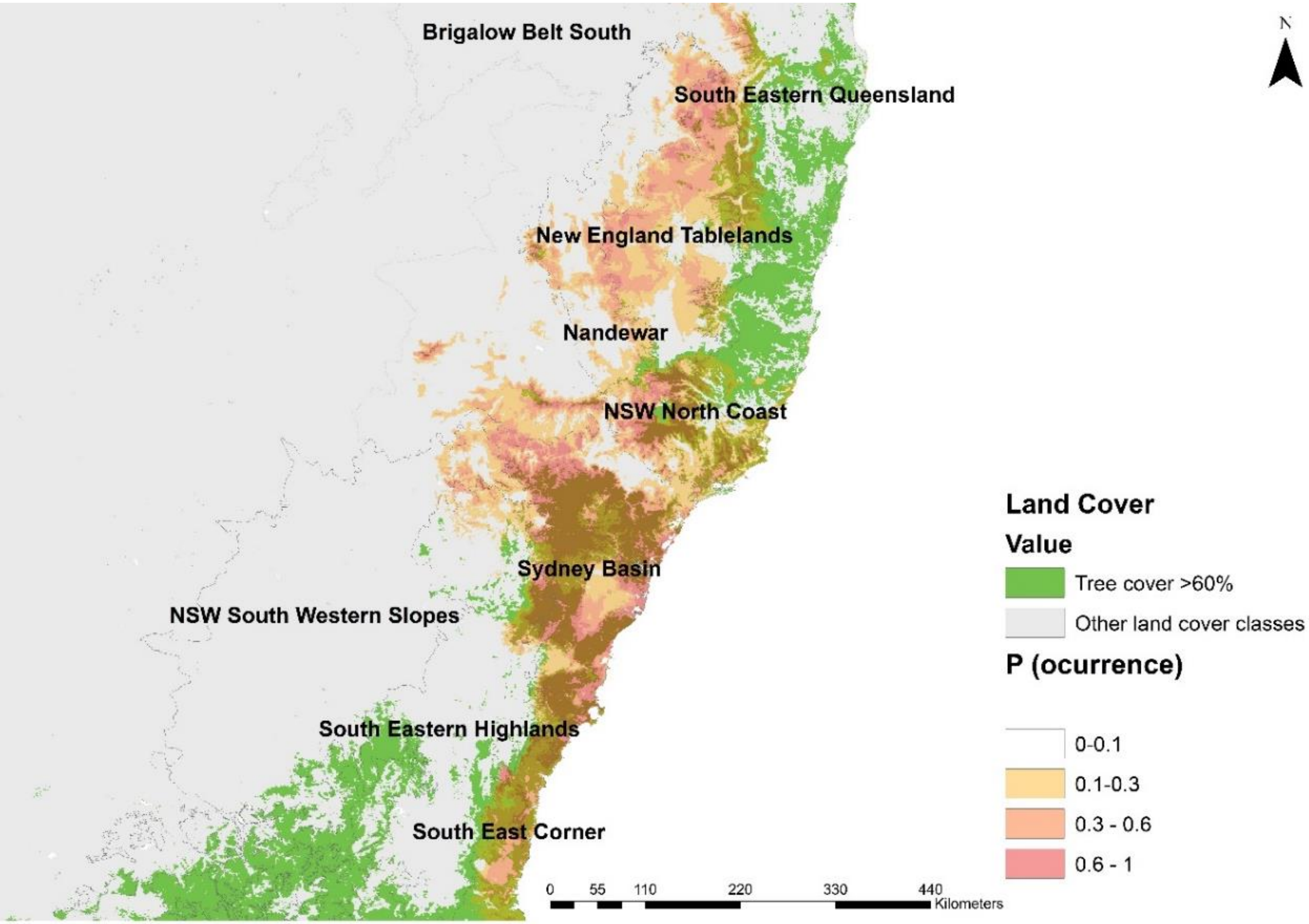


Figure 23. Predicted distribution of the velvet gecko (*Amalosia lesueurii)* for current time with a land cover base layer.

I found that under every emission scenario, velvet geckos will experience greater range contractions than expansions (Figure 24). The largest range contractions are predicted to occur in the Sydney Basin region and New England Tablelands (Figure 25). Nonetheless, the species is predicted to persist in higher elevation refugia, with range expansions in the south eastern highlands and the NSW South Western Slopes bioregions (Figure 25).

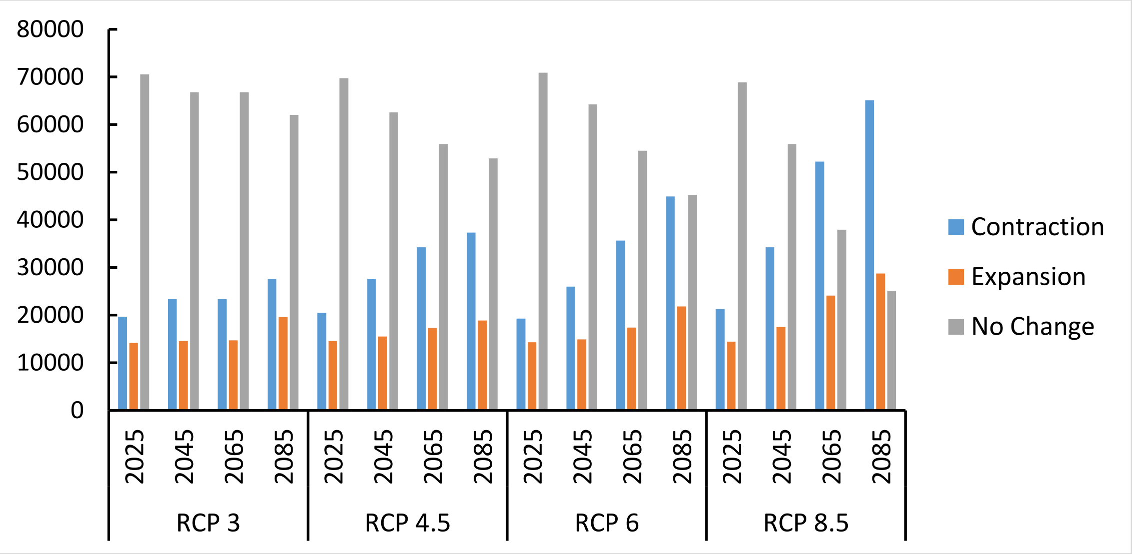


Figure 24. Future changes on species distribution under different emission scenarios, showing the amount of area with no change, contraction or expansion for all the projected years.

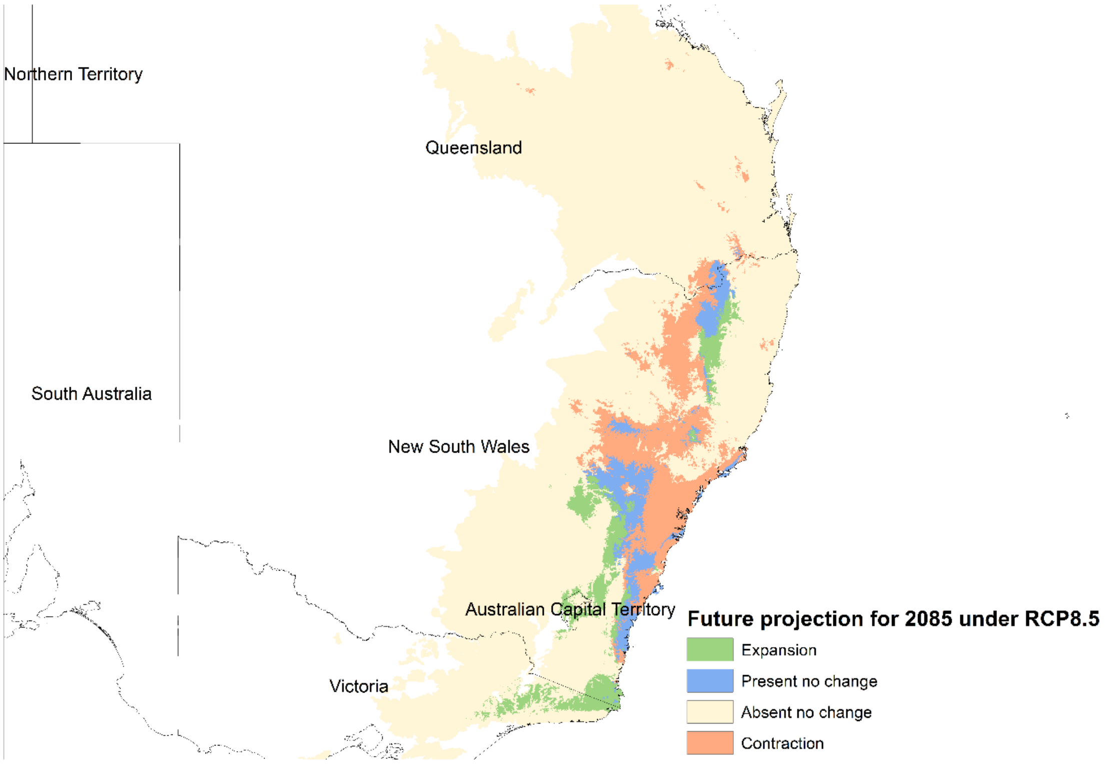


Figure 25. Projected future distribution of the velvet gecko for 2085 under RCP 8.5 emission scenario.

3.5. Discussion

Species are predicted to respond to climatic changes via shifts in distribution. In this study, I used environmental niche modelling to explore how the geographic range of the velvet gecko might respond to future changes in climate. Under the RCP 8.5 scenario, the species is predicted to lose 54% of its current range, with significant loss from the Sydney Basin region (Figure 25). By contrast, range expansion is predicted to occur in the Brigalow Belt South bioregion, the New England Tablelands region, and the NSW South Western Slopes bioregion. However, the underlying assumption of ENMs is that species can track shifting climates via dispersal. For the velvet gecko, such shifts are unlikely to occur for two reasons. First, the range expansions are predicted to occur in fragmented agricultural landscapes (Figure 23 and Figure 25). Second, previous mark-recapture and genetic studies suggest that velvet geckos have poor dispersal abilities, even in intact landscapes (Dubey *et al.*, 2012). Thus, it is unlikely that this species will be able to disperse to suitable areas to track future shifts in climate throughout much of its current range.

These findings disagree with those of a recent study that also used MaxEnt to model the potential distribution of *A. lesueurii*. In that study, the potential distribution included all coastal areas of NSW, and there was no range contraction in NSW under future climatic scenarios (Bezeng, Tesfamichael and Dayananda, 2018). By contrast, my results produced a more restricted current distribution, with a very small area predicted on the NSW north coast (see Figure 22). Furthermore, while Bezeng et al. (2018) predicted a range expansion for the species, I found a substantial loss of range under every emission scenario (e.g. Figure 25).

Why do my results differ from those of Bezeng et al. (2018)? Notably, there are substantial methodological differences in the nature of the predictive bioclimatic variables used to generate model results, and in the methods that were used to rank candidate models. For example, Bezeng et al. (2018) found that the minimum temperature of the coldest month, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation of wettest quarter, precipitation of driest quarter, and precipitation of warmest quarter were the most important predictor variables. By contrast, I found that the best predictors of the species current distribution was the mean temperature of the warmest quarter, followed by the mean temperature of the wettest quarter, precipitation of the driest month, maximum temperature of warmest month, and precipitation of warmest quarter.

Notably, the most important predictor variable in my models was the mean temperature of the warmest quarter. Velvet geckos oviposit in early November, and the incubation period of 100 days extends over the summer (Doughty, 1997; Pike, Webb and Shine, 2010). Considering that the embryonic life stages of the velvet gecko are strongly affected by incubation temperatures (Dayananda *et al*., 2016; Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017; Abayarathna, Murray and Webb, 2019), and that ambient temperatures strongly influence incubation temperatures (Chapter 2), it is not surprising that the temperature of the warmest quarter was a good predictor of the species' range. For example, I found a strong positive correlation between maximum daily air temperatures and nest temperatures (Chapter 2). At sites north of Sydney, temperatures in some nests exceeded the species critical thermal maximum for several hours per day during the incubation period. That is, under warmer conditions, nests will be hotter, which could adversely affect hatching success of eggs or produce smaller, less fit offspring (Dayananda *et al.*, 2016; Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017). My predictions of the projected species distribution showed large contractions in the northern part of the range, with most of QLD predicted climatic suitable areas disappearing, and within the New England Tablelands and around the conjunction of Brigalow Belt south, Nandewar and NSW North Coast. In this sense, contractions of northern populations may occur because of the effects on nest temperatures, rather than on effects on other life stages.

Precipitation variables were also a strong predictor of the species distribution. Precipitation is known to affect prey availability in forests (Madsen and Shine, 2000), so that drier conditions may affect the ability of females to procure resources for reproduction. Alternatively, dry conditions might lead to desiccation of eggs in nests, as velvet geckos lay parchment shelled eggs that have high rates of water exchange, and thus, are prone to desiccation (Thompson *et al.*, 1996). Future studies to explore how humidity and temperature interact to influence hatching success are necessary to test this hypothesis.

In contrast to a previous study (Bezeng, Tesfamichael and Dayananda, 2018), my results showed that under future climates, the biggest range contraction is likely to occur in the Sydney Basin (Figure 25). Loss of velvet geckos from this region is likely to have significant effects on the threatened broad-headed snake *Hoplocephalus bungaroides*. This snake species is entirely restricted to sandstone rock outcrops in the Sydney Basin, and juveniles feed mostly on small lizards, with > 70% of the diet comprising velvet geckos (Webb & Shine, 1998). Modelling of the broad-headed snakes distribution suggests that it too will suffer range contractions under climate change (Penman et al., 2010). These range contractions, coupled with loss of a major prey of the juvenile life stage, is likely to adversely affect the resilience of populations to other threats. For example, elasticity analyses of vital rates showed that broad-headed snake populations are most sensitive to perturbation of juvenile and adult survival; that is, factors that decrease survival of these age-classes can drive populations towards extinction (Webb, Brook and Shine, 2002). Studies on other snake species have found that prey availability can substantially affect growth, survival and reproduction (e.g. Madsen & Shine, 2000). Loss of velvet geckos will therefore likely negatively affect growth rates and survival of juvenile broad-headed snakes, and in concert with existing threats such as bush-rock collection and illegal collection of snakes (Shine *et al.*, 1998; Webb, Brook and Shine, 2002), poses a serious threat to the persistence of this species.

In conclusion, I used ENMs to explore how future climates might affect the geographic range of a widespread nocturnal gecko. In contrast to a previous study, I found significant range contractions under future climates, with loss of the species from its current stronghold in the Sydney Basin bioregion. While range expansions are predicted to occur, such range shifts are unlikely to occur in highly fragmented parts of the northern range. This underscores the importance of considering how multiple stressors will effect persistence of ectotherms. For most Australian reptiles, habitat loss and destruction remain the greatest threat to future persistence (Webb, Harlow and Pike, 2015). Finally, my findings suggest that loss of velvet geckos from the Sydney Basin will have important ramifications for the persistence of one of Australia's most endangered snakes. My findings also highlight why it is important to study common, widely distributed and abundant species such as the velvet gecko.

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Appendix

Table 5. Correlation between bioclimatic variables used for the species distribution modelling.

Variable	**Altitude**	**B01**	**B02**	**B03**	**B04**	**B05**	**B06**	**B07**	**B08**	**B09**	**B10**	**B11**	**B12**	**B13**	**B14**	**B15**	**B16**	**B17**	**B18**	**B19**
Altitude	1	-0.899	0.359	-0.492	0.555	-0.042	-0.843	0.477	-0.336	-0.644	-0.537	-0.952	-0.270	-0.275	-0.171	-0.132	-0.231	-0.126	-0.097	-0.253
B01	-0.899	1	-0.069	0.606	-0.278	0.359	0.685	-0.195	0.567	0.688	0.807	0.897	0.017	0.076	-0.127	0.228	0.027	-0.142	-0.069	0.011
B02	0.359	-0.069	1	0.377	0.948	0.893	-0.766	0.984	0.684	-0.281	0.512	-0.487	-0.866	-0.696	-0.891	0.175	-0.723	-0.875	-0.578	-0.895
B03	-0.492	0.606	0.377	1	0.080	0.513	0.165	0.206	0.614	0.387	0.633	0.435	-0.250	-0.112	-0.330	0.269	-0.196	-0.333	-0.211	-0.262
B04	0.555	-0.278	0.948	0.080	1	0.790	-0.873	0.986	0.539	-0.410	0.341	-0.671	-0.859	-0.729	-0.838	0.055	-0.737	-0.816	-0.580	-0.861
B05	-0.042	0.359	0.893	0.513	0.790	1	-0.421	0.842	0.897	0.014	0.836	-0.085	-0.826	-0.655	-0.898	0.218	-0.696	-0.893	-0.603	-0.846
B06	-0.843	0.685	-0.766	0.165	-0.873	-0.421	1	-0.844	-0.125	0.639	0.134	0.929	0.639	0.552	0.580	0.003	0.534	0.557	0.365	0.666
B07	0.477	-0.195	0.984	0.206	0.986	0.842	-0.844	1	0.604	-0.373	0.414	-0.603	-0.870	-0.717	-0.877	0.127	-0.730	-0.861	-0.574	-0.897
B08	-0.336	0.567	0.684	0.614	0.539	0.897	-0.125	0.604	1	0.146	0.883	0.195	-0.684	-0.517	-0.747	0.226	-0.571	-0.783	-0.526	-0.720
B09	-0.644	0.688	-0.281	0.387	-0.410	0.014	0.639	-0.373	0.146	1	0.425	0.718	0.307	0.317	0.207	0.046	0.250	0.254	0.140	0.380
B10	-0.537	0.807	0.512	0.633	0.341	0.836	0.134	0.414	0.883	0.425	1	0.465	-0.512	-0.380	-0.638	0.245	-0.430	-0.638	-0.430	-0.515
B11	-0.952	0.897	-0.487	0.435	-0.671	-0.085	0.929	-0.603	0.195	0.718	0.465	1	0.402	0.385	0.290	0.134	0.349	0.267	0.201	0.405
B12	-0.270	0.017	-0.866	-0.250	-0.859	-0.826	0.639	-0.870	-0.684	0.307	-0.512	0.402	1	0.946	0.912	0.167	0.950	0.910	0.874	0.908
B13	-0.275	0.076	-0.696	-0.112	-0.729	-0.655	0.552	-0.717	-0.517	0.317	-0.380	0.385	0.946	1	0.763	0.452	0.990	0.757	0.962	0.753
B14	-0.171	-0.127	-0.891	-0.330	-0.838	-0.898	0.580	-0.877	-0.747	0.207	-0.638	0.290	0.912	0.763	1	-0.195	0.764	0.979	0.656	0.956
B15	-0.132	0.228	0.175	0.269	0.055	0.218	0.003	0.127	0.226	0.046	0.245	0.134	0.167	0.452	-0.195	1	0.455	-0.216	0.570	-0.209
B16	-0.231	0.027	-0.723	-0.196	-0.737	-0.696	0.534	-0.730	-0.571	0.250	-0.430	0.349	0.950	0.990	0.764	0.455	1	0.753	0.975	0.744
B17	-0.126	-0.142	-0.875	-0.333	-0.816	-0.893	0.557	-0.861	-0.783	0.254	-0.638	0.267	0.910	0.757	0.979	-0.216	0.753	1	0.646	0.983
B18	-0.097	-0.069	-0.578	-0.211	-0.580	-0.603	0.365	-0.574	-0.526	0.140	-0.430	0.201	0.874	0.962	0.656	0.570	0.975	0.646	1	0.617
B19	-0.253	0.011	-0.895	-0.262	-0.861	-0.846	0.666	-0.897	-0.720	0.380	-0.515	0.405	0.908	0.753	0.956	-0.209	0.744	0.983	0.617	1

Table 6. Parameters, AIC, and delta AIC for the candidate models. Feature classes as follows, linear (L), quadratic (Q), product (P), hinge (H) and threshold (T).

Feature class	RM	AICc	Delta AICc	Parameters
H	0.1	17421.280	930.792	238
H	0.2	16737.571	247.082	197
H	0.3	16604.571	114.083	165
H	0.4	16564.781	74.292	150
H	0.5	16525.177	34.689	131
H	0.6	16516.766	26.277	120
H	0.7	16500.682	10.194	109
H	0.8	16534.616	44.128	117
H	0.9	16498.853	8.365	101
H	1	16490.488	0.000	95
H	2	16512.632	22.143	68
H	4	16561.348	70.860	45
H	5	16585.762	95.274	45
H	6	16594.596	104.107	40
H	8	16649.027	158.539	45
H	10	16686.740	196.251	41
HP	0.1	18818.930	2273.216	254
HP	0.2	17749.961	1204.247	213
HP	0.3	16694.881	149.167	177
HP	0.4	16542.744	132.761	150
HP	0.5	16513.087	103.104	140
HP	0.6	16450.022	40.039	122
HP	0.7	16437.880	27.897	115
HP	0.8	16422.485	12.502	107
HP	0.9	16423.389	13.407	102
HP	1	16415.538	5.555	92
HP	2	16444.670	34.687	68
HP	4	16522.567	112.584	45
HP	5	16560.755	150.772	39
HP	6	16613.703	203.720	42
HP	8	16622.944	212.961	28
HP	10	16676.665	266.682	30
HPT	0.1	18818.930	2408.948	254
HPT	0.2	17749.961	1339.978	213
HPT	0.3	16694.881	284.898	177
HPT	0.4	16542.744	132.761	150
HPT	0.5	16513.087	103.104	140
HPT	0.6	16450.022	40.039	122
HPT	0.7	16437.880	27.897	115
HPT	0.8	16422.485	12.502	107
HPT	0.9	16423.389	13.407	102
HPT	1	16415.538	5.555	92
HPT	2	16444.670	34.687	68
HPT	4	16522.567	112.584	45
HPT	5	16560.755	150.772	39
HPT	6	16613.703	203.720	42
HPT	8	16622.944	212.961	28
HPT	10	16676.665	266.682	30
HT	0.1	18763.468	2217.754	259
HT	0.2	17764.420	1218.706	217
HT	0.3	16811.326	265.612	180
HT	0.4	16620.218	210.235	160

HT	0.5	16556.131	146.148	141
HT	0.6	16526.879	116.896	128
HT	0.7	16512.803	102.820	119
HT	0.8	16512.937	102.954	113
HT	0.9	16479.930	69.947	97
HT	1	16490.160	80.177	97
HT	2	16518.767	108.784	64
HT	4	16626.744	216.762	56
HT	5	16642.155	232.172	50
HT	6	16656.028	246.045	44
HT	8	16698.458	288.475	41
HT	10	16745.739	335.756	39
L	0.1	17522.122	176.338	11
L	0.2	17524.722	178.938	11
L	0.3	17526.187	180.404	10
L	0.4	17527.590	181.806	10
L	0.5	17528.196	182.413	10
L	0.6	17527.214	181.431	9
L	0.7	17528.179	182.396	9
L	0.8	17528.665	182.881	9
L	0.9	17530.102	184.318	9
L	1	17530.190	184.407	9
L	2	17540.727	194.943	9
L	4	17566.263	220.479	8
L	5	17583.515	237.732	8
L	6	17601.061	255.278	8
L	8	17641.976	296.192	8
L	10	17686.508	340.724	7
LH	0.1	17887.848	1406.842	242
LH	0.2	16824.741	343.735	207
LH	0.3	16604.571	123.565	165
LH	0.4	16564.781	83.775	150
LH	0.5	16537.008	56.002	135
LH	0.6	16516.766	35.760	120
LH	0.7	16544.072	63.066	124
LH	0.8	16524.579	43.573	114
LH	0.9	16493.989	12.983	101
LH	1	16481.006	0.000	91
LH	2	16486.754	5.748	59
LH	4	16520.042	39.036	41
LH	5	16547.852	66.846	43
LH	6	16559.929	78.923	36
LH	8	16607.756	126.750	38
LH	10	16651.600	170.594	38
LHP	0.1	19098.327	2552.613	244
LHP	0.2	17783.776	1238.062	229
LHP	0.3	16691.935	146.221	160
LHP	0.4	16551.540	141.558	152
LHP	0.5	16535.256	125.273	149
LHP	0.6	16519.981	109.998	142
LHP	0.7	16476.543	66.560	125
LHP	0.8	16452.715	42.732	115
LHP	0.9	16432.843	22.860	103
LHP	1	16409.983	0.000	93
LHP	2	16444.114	34.132	68
LHP	4	16523.451	113.468	48

LHP	5	16563.955	153.972	39
LHP	6	16619.570	209.587	45
LHP	8	16634.270	224.287	33
LHP	10	16700.598	290.615	41
LHPT	0.1	19098.327	2688.344	244
LHPT	0.2	17783.776	1373.793	229
LHPT	0.3	16691.935	281.952	160
LHPT	0.4	16551.540	141.558	152
LHPT	0.5	16535.256	125.273	149
LHPT	0.6	16519.981	109.998	142
LHPT	0.7	16476.543	66.560	125
LHPT	0.8	16452.715	42.732	115
LHPT	0.9	16432.843	22.860	103
LHPT	1	16409.983	0.000	93
LHPT	2	16444.114	34.132	68
LHPT	4	16523.451	113.468	48
LHPT	5	16563.955	153.972	39
LHPT	6	16619.570	209.587	45
LHPT	8	16634.270	224.287	33
LHPT	10	16700.598	290.615	41
LHT	0.1	18940.644	2530.662	251
LHT	0.2	17534.065	1124.082	218
LHT	0.3	16771.084	361.102	188
LHT	0.4	16547.302	137.319	139
LHT	0.5	16594.667	184.684	154
LHT	0.6	16550.755	140.773	136
LHT	0.7	16547.076	137.093	130
LHT	0.8	16520.955	110.972	116
LHT	0.9	16495.913	85.930	104
LHT	1	16477.325	67.342	92
LHT	2	16532.489	122.507	68
LHT	4	16573.239	163.256	41
LHT	5	16604.278	194.295	41
LHT	6	16629.328	219.345	39
LHT	8	16663.689	253.706	35
LHT	10	16716.777	306.794	38
LP	0.1	16497.367	16.361	47
LP	0.2	16553.293	72.287	48
LP	0.3	16528.502	47.496	47
LP	0.4	16532.293	51.287	41
LP	0.5	16521.587	40.581	39
LP	0.6	16584.959	103.953	39
LP	0.7	16589.427	108.421	38
LP	0.8	16597.261	116.255	29
LP	0.9	16629.998	148.992	35
LP	1	16663.811	182.805	33
LP	2	16749.836	268.830	21
LP	4	16934.476	453.470	11
LP	5	17005.235	524.229	11
LP	6	17082.487	601.481	10
LP	8	17225.149	744.143	9
LP	10	17320.086	839.080	9
LPT	0.1	16614.244	204.261	50
LPT	0.2	16512.033	102.050	49
LPT	0.3	16561.391	151.408	47
LPT	0.4	16583.261	173.278	39

LPT	0.5	16629.655	219.672	40
LPT	0.6	16605.570	195.587	39
LPT	0.7	16639.205	229.222	37
LPT	0.8	16625.028	215.045	33
LPT	0.9	16677.201	267.218	36
LPT	1	16693.949	283.967	30
LPT	2	16815.943	405.960	20
LPT	4	16980.674	570.691	11
LPT	5	17052.022	642.039	10
LPT	6	17125.959	715.976	10
LPT	8	17245.976	835.993	9
LPT	10	17337.148	927.165	9
LQ	0.1	16606.808	125.802	21
LQ	0.2	16593.818	112.812	21
LQ	0.3	16600.918	119.912	20
LQ	0.4	16613.727	132.721	19
LQ	0.5	16628.941	147.935	21
LQ	0.6	16633.670	152.664	20
LQ	0.7	16627.501	146.495	20
LQ	0.8	16624.910	143.905	22
LQ	0.9	16666.408	185.402	21
LQ	1	16678.619	197.613	21
LQ	2	16794.131	313.125	16
LQ	4	17079.287	598.281	11
LQ	5	17169.741	688.735	10
LQ	6	17231.637	750.631	9
LQ	8	17285.604	804.598	8
LQ	10	17331.827	850.822	7
LQH	0.1	19068.944	2523.230	260
LQH	0.2	17920.664	1374.950	208
LQH	0.3	16764.216	218.501	179
LQH	0.4	16612.121	202.138	157
LQH	0.5	16594.667	184.684	154
LQH	0.6	16559.055	149.073	138
LQH	0.7	16548.467	138.484	131
LQH	0.8	16525.467	115.484	118
LQH	0.9	16499.813	89.830	105
LQH	1	16480.986	71.003	95
LQH	2	16529.097	119.114	70
LQH	4	16553.476	143.493	36
LQH	5	16580.080	170.097	37
LQH	6	16609.341	199.358	39
LQH	8	16654.061	244.078	36
LQH	10	16702.331	292.348	35
LQHP	0.1	18941.432	2531.449	249
LQHP	0.2	17962.997	1553.014	202
LQHP	0.3	16755.373	345.390	167
LQHP	0.4	16525.315	115.332	145
LQHP	0.5	16504.174	94.192	137
LQHP	0.6	16483.914	73.931	133
LQHP	0.7	16445.447	35.464	113
LQHP	0.8	16417.546	7.563	103
LQHP	0.9	16442.580	32.597	109
LQHP	1	16421.700	11.717	98
LQHP	2	16429.196	19.213	62
LQHP	4	16495.212	85.229	40

LQHP	5	16552.396	142.413	41
LQHP	6	16590.730	180.747	38
LQHP	8	16640.522	230.539	38
LQHP	10	16684.887	274.904	35
LQHPT	0.1	18941.432	2531.449	249
LQHPT	0.2	17962.997	1553.014	202
LQHPT	0.3	16755.373	345.390	167
LQHPT	0.4	16525.315	115.332	145
LQHPT	0.5	16504.174	94.192	137
LQHPT	0.6	16483.914	73.931	133
LQHPT	0.7	16445.447	35.464	113
LQHPT	0.8	16417.546	7.563	103
LQHPT	0.9	16442.580	32.597	109
LQHPT	1	16421.700	11.717	98
LQHPT	2	16429.196	19.213	62
LQHPT	4	16495.212	85.229	40
LQHPT	5	16552.396	142.413	41
LQHPT	6	16590.730	180.747	38
LQHPT	8	16640.522	230.539	38
LQHPT	10	16684.887	274.904	35
LQHT	0.1	19068.944	2658.961	260
LQHT	0.2	17920.664	1510.681	208
LQHT	0.3	16764.216	354.233	179
LQHT	0.4	16612.121	202.138	157
LQHT	0.5	16594.667	184.684	154
LQHT	0.6	16559.055	149.073	138
LQHT	0.7	16548.467	138.484	131
LQHT	0.8	16525.467	115.484	118
LQHT	0.9	16499.813	89.830	105
LQHT	1	16480.986	71.003	95
LQHT	2	16529.097	119.114	70
LQHT	4	16553.476	143.493	36
LQHT	5	16580.080	170.097	37
LQHT	6	16609.341	199.358	39
LQHT	8	16654.061	244.078	36
LQHT	10	16702.331	292.348	35
LQP	0.1	16590.557	44.843	54
LQP	0.2	16589.842	44.128	52
LQP	0.3	16545.714	0.000	48
LQP	0.4	16537.145	127.162	41
LQP	0.5	16559.935	149.952	39
LQP	0.6	16599.782	189.799	44
LQP	0.7	16612.699	202.716	43
LQP	0.8	16645.675	235.692	41
LQP	0.9	16631.707	221.724	37
LQP	1	16653.852	243.869	32
LQP	2	16785.376	375.394	22
LQP	4	16937.532	527.549	15
LQP	5	16991.746	581.763	14
LQP	6	17041.545	631.562	12
LQP	8	17138.671	728.688	9
LQP	10	17209.499	799.516	8
LQPT	0.1	16590.557	180.575	54
LQPT	0.2	16589.842	179.859	52
LQPT	0.3	16545.714	135.731	48
LQPT	0.4	16537.145	127.162	41

LQPT	0.5	16559.935	149.952	39
LQPT	0.6	16599.782	189.799	44
LQPT	0.7	16612.699	202.716	43
LQPT	0.8	16645.675	235.692	41
LQPT	0.9	16631.707	221.724	37
LQPT	1	16653.852	243.869	32
LQPT	2	16785.376	375.394	22
LQPT	4	16937.532	527.549	15
LQPT	5	16991.746	581.763	14
LQPT	6	17041.545	631.562	12
LQPT	8	17138.671	728.688	9
LQPT	10	17209.499	799.516	8
LQT	0.1	16642.469	96.755	21
LQT	0.2	16636.761	91.047	20
LQT	0.3	16640.300	94.586	20
LQT	0.4	16609.957	199.974	19
LQT	0.5	16663.208	253.225	18
LQT	0.6	16628.755	218.773	19
LQT	0.7	16667.867	257.884	17
LQT	0.8	16700.179	290.196	18
LQT	0.9	16697.251	287.268	18
LQT	1	16724.353	314.370	19
LQT	2	16864.763	454.781	14
LQT	4	17125.231	715.248	10
LQT	5	17187.565	777.582	10
LQT	6	17226.570	816.587	9
LQT	8	17275.417	865.434	8
LQT	10	17319.154	909.171	8
LT	0.1	17522.122	1041.116	11
LT	0.2	17524.722	1043.716	11
LT	0.3	17526.187	1045.181	10
LT	0.4	17527.590	1046.584	10
LT	0.5	17528.196	1047.190	10
LT	0.6	17527.214	1046.208	9
LT	0.7	17528.179	1047.173	9
LT	0.8	17528.665	1047.659	9
LT	0.9	17530.102	1049.096	9
LT	1	17530.190	1049.184	9
LT	2	17540.727	1059.721	9
LT	4	17566.263	1085.257	8
LT	5	17583.515	1102.509	8
LT	6	17601.061	1120.055	8
LT	8	17641.976	1160.970	8
LT	10	17686.508	1205.502	7
P	0.1	16589.032	98.544	41
P	0.2	16596.250	105.762	42
P	0.3	16617.368	126.879	37
P	0.4	16619.863	129.374	33
P	0.5	16629.066	138.578	33
P	0.6	16603.498	113.010	30
P	0.7	16629.867	139.379	29
P	0.8	16647.255	156.767	28
P	0.9	16652.804	162.316	25
P	1	16643.032	152.543	27
P	2	16778.805	288.317	17
P	4	16935.594	445.106	12

P	5	17013.565	523.077	11
P	6	17092.902	602.414	11
P	8	17247.277	756.789	10
P	10	17331.148	840.660	8
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PT	0.2	16648.840	103.126	37
PT	0.3	16665.953	120.239	35
PT	0.4	16698.732	288.749	35
PT	0.5	16688.100	278.117	30
PT	0.6	16700.175	290.192	28
PT	0.7	16700.474	290.491	29
PT	0.8	16728.642	318.659	30
PT	0.9	16728.653	318.670	26
PT	1	16752.088	342.105	23
PT	2	16826.953	416.970	15
PT	4	16988.027	578.044	12
PT	5	17068.081	658.099	11
PT	6	17143.061	733.078	11
PT	8	17274.744	864.761	8
PT	10	17349.482	939.499	8
Q	0.1	17345.783	0.000	10
Q	0.2	17349.807	4.023	11
Q	0.3	17348.809	3.025	10
Q	0.4	17350.813	5.030	10
Q	0.5	17349.609	3.826	9
Q	0.6	17350.378	4.595	9
Q	0.7	17351.114	5.330	9
Q	0.8	17351.449	5.665	9
Q	0.9	17352.110	6.327	9
Q	1	17353.064	7.281	9
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Q	4	17390.916	45.132	7
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Q	6	17433.780	87.996	8
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Q	10	17496.484	150.701	6
QH	0.1	19089.252	2543.537	238
QH	0.2	18040.302	1494.587	228
QH	0.3	16764.216	218.501	179
QH	0.4	16576.804	166.821	149
QH	0.5	16556.131	146.148	141
QH	0.6	16513.833	103.850	123
QH	0.7	16512.803	102.820	119
QH	0.8	16551.521	141.538	127
QH	0.9	16504.857	94.875	107
QH	1	16470.266	60.284	90
QH	2	16515.656	105.674	63
QH	4	16556.591	146.609	37
QH	5	16571.390	161.408	34
QH	6	16592.763	182.780	34
QH	8	16661.974	251.991	39
QH	10	16705.718	295.735	35
QHP	0.1	19165.660	2755.677	257
QHP	0.2	18132.981	1722.998	219
QHP	0.3	16754.301	344.319	177
QHP	0.4	16532.236	122.254	145

QHP	0.5	16503.760	93.777	141
QHP	0.6	16472.568	62.585	128
QHP	0.7	16465.596	55.613	123
QHP	0.8	16447.446	37.463	111
QHP	0.9	16428.778	18.795	106
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QHP	2	16439.429	29.446	63
QHP	4	16509.607	99.624	46
QHP	5	16555.501	145.518	42
QHP	6	16599.063	189.080	40
QHP	8	16640.243	230.260	38
QHP	10	16705.972	295.989	44
QHPT	0.1	19165.660	2755.677	257
QHPT	0.2	18132.981	1722.998	219
QHPT	0.3	16754.301	344.319	177
QHPT	0.4	16532.236	122.254	145
QHPT	0.5	16503.760	93.777	141
QHPT	0.6	16472.568	62.585	128
QHPT	0.7	16465.596	55.613	123
QHPT	0.8	16447.446	37.463	111
QHPT	0.9	16428.778	18.795	106
QHPT	1	16420.311	10.328	96
QHPT	2	16439.429	29.446	63
QHPT	4	16509.607	99.624	46
QHPT	5	16555.501	145.518	42
QHPT	6	16599.063	189.080	40
QHPT	8	16640.243	230.260	38
QHPT	10	16705.972	295.989	44
QHT	0.1	19089.252	2679.269	238
QHT	0.2	18040.302	1630.319	228
QHT	0.3	16764.216	354.233	179
QHT	0.4	16576.804	166.821	149
QHT	0.5	16556.131	146.148	141
QHT	0.6	16513.833	103.850	123
QHT	0.7	16512.803	102.820	119
QHT	0.8	16551.521	141.538	127
QHT	0.9	16504.857	94.875	107
QHT	1	16470.266	60.284	90
QHT	2	16515.657	105.674	63
QHT	4	16556.591	146.609	37
QHT	5	16571.390	161.408	34
QHT	6	16592.763	182.780	34
QHT	8	16661.974	251.991	39
QHT	10	16705.718	295.735	35
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QP	0.4	16663.147	253.164	37
QP	0.5	16669.253	259.270	34
QP	0.6	16683.389	273.406	30
QP	0.7	16685.271	275.288	33
QP	0.8	16706.924	296.941	32
QP	0.9	16698.309	288.326	30
QP	1	16681.350	271.367	21
QP	2	16795.013	385.030	23
QP	4	16939.896	529.913	16

QP	5	16996.652	586.669	13
QP	6	17047.588	637.605	12
QP	8	17139.170	729.187	10
QP	10	17209.637	799.654	9
QPT	0.1	16670.068	260.085	48
QPT	0.2	16653.763	243.780	40
QPT	0.3	16649.459	239.476	37
QPT	0.4	16663.147	253.164	37
QPT	0.5	16669.253	259.270	34
QPT	0.6	16683.389	273.406	30
QPT	0.7	16685.271	275.288	33
QPT	0.8	16706.924	296.941	32
QPT	0.9	16698.309	288.326	30
QPT	1	16681.350	271.367	21
QPT	2	16795.013	385.030	23
QPT	4	16939.896	529.913	16
QPT	5	16996.652	586.669	13
QPT	6	17047.588	637.605	12
QPT	8	17139.170	729.187	10
QPT	10	17209.637	799.654	9
QT	0.1	17369.090	823.376	10
QT	0.2	17367.857	822.143	11
QT	0.3	17366.224	820.510	11
QT	0.4	17364.397	954.414	11
QT	0.5	17364.208	954.225	11
QT	0.6	17363.326	953.343	10
QT	0.7	17361.239	951.256	9
QT	0.8	17362.424	952.441	9
QT	0.9	17363.393	953.411	9
QT	1	17360.973	950.990	7
QT	2	17368.774	958.791	8
QT	4	17396.317	986.334	8
QT	5	17411.091	1001.108	8
QT	6	17424.201	1014.218	7
QT	8	17463.340	1053.357	7
QT	10	17488.423	1078.440	6

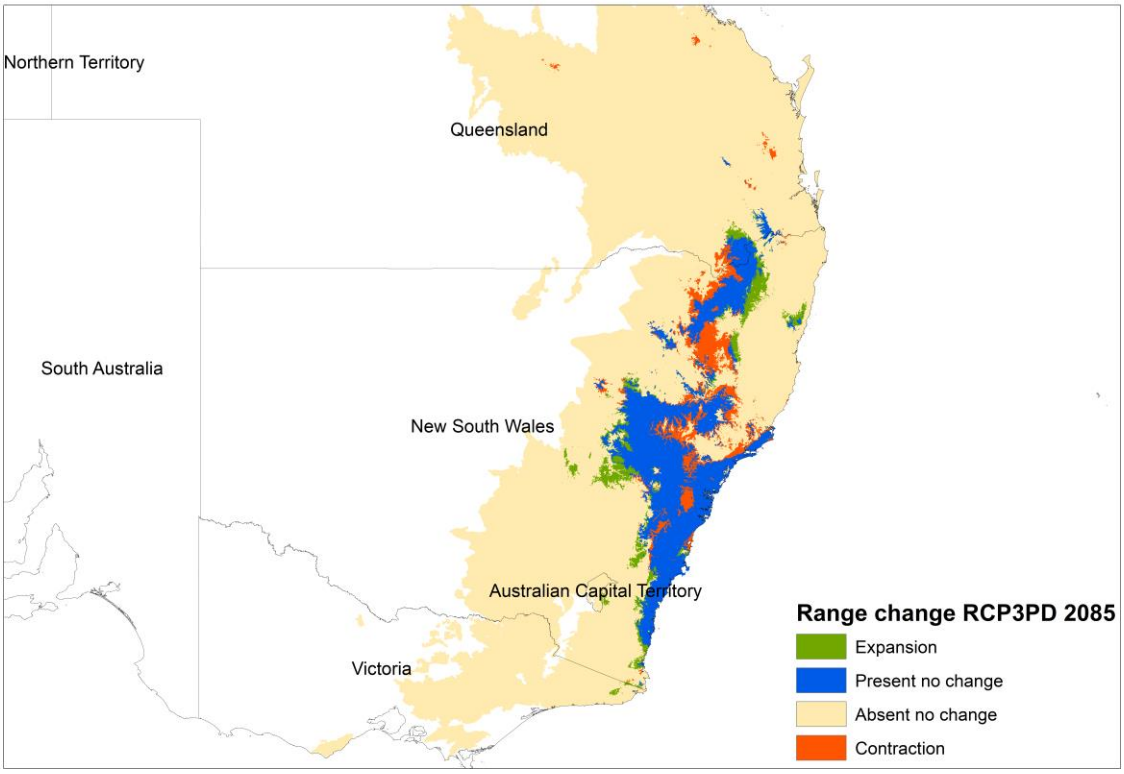

Figure 26. Projected future distribution of the velvet gecko for 2085 under RCP 3PD emission scenario.

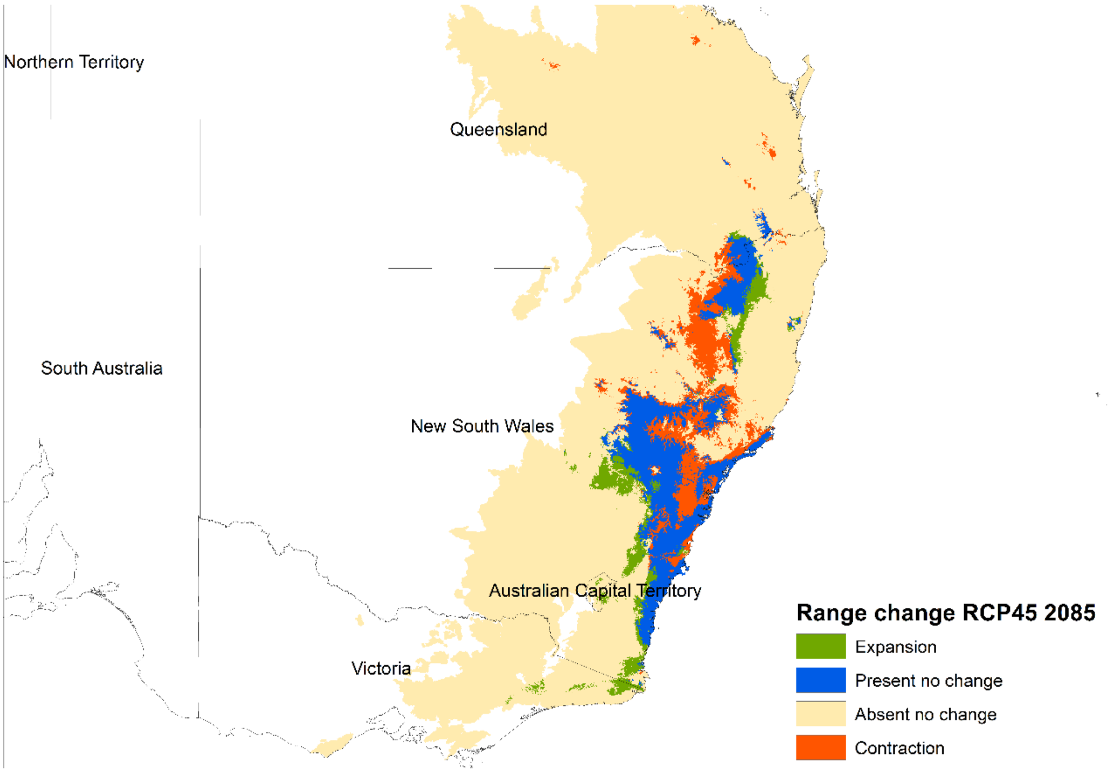

Figure 27. Projected future distribution of the velvet gecko for 2085 under RCP 4.5 emission scenario.

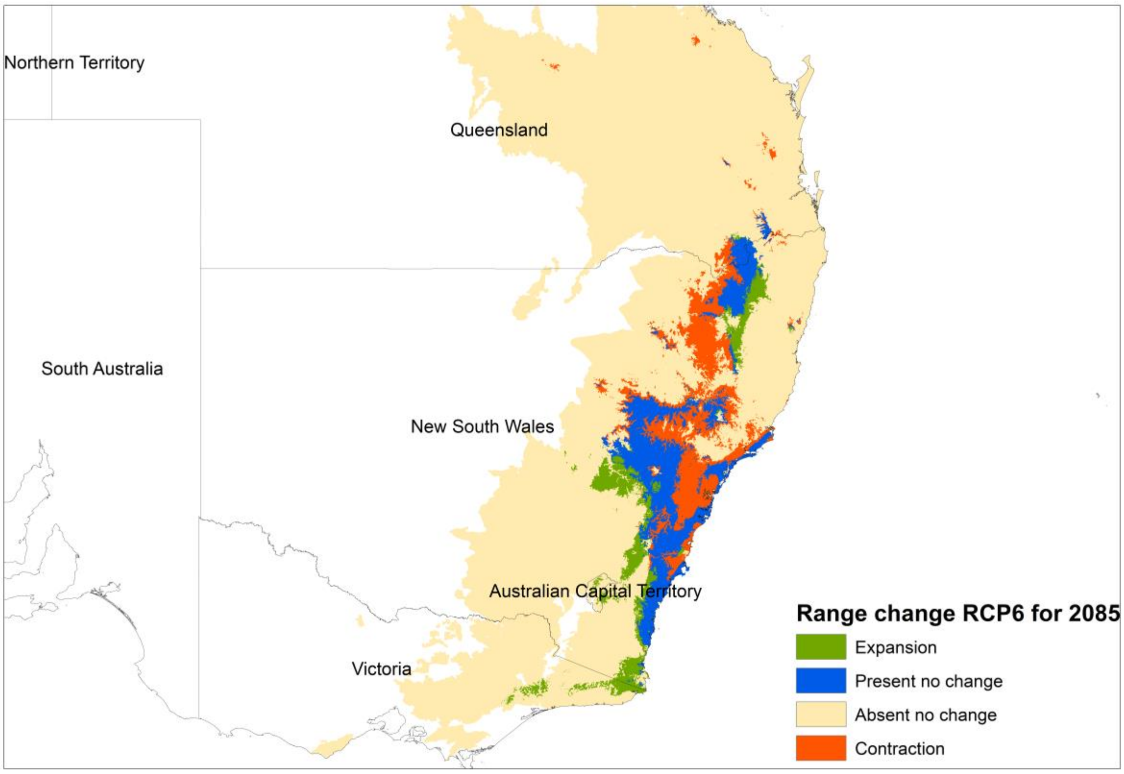

Figure 28. Projected future distribution of the velvet gecko for 2085 under RCP 6 emission scenario.

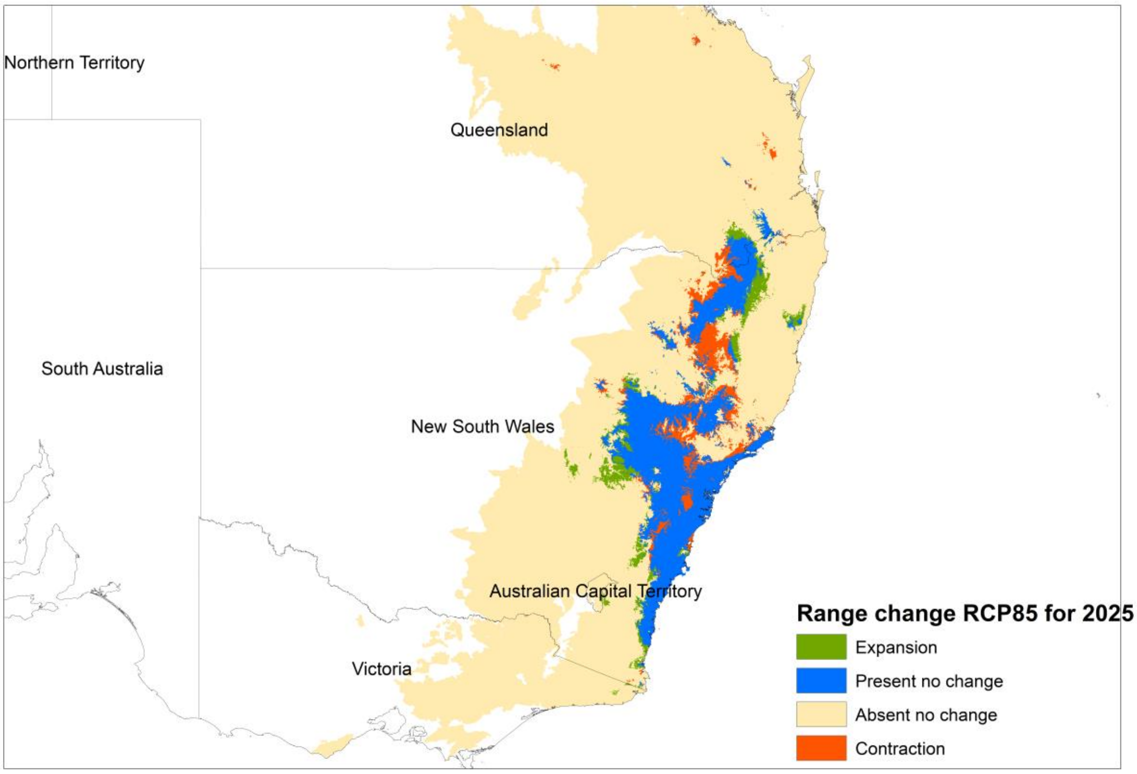

Figure 29. Projected future distribution of the velvet gecko for 2025 under RCP 8.5 emission scenario.

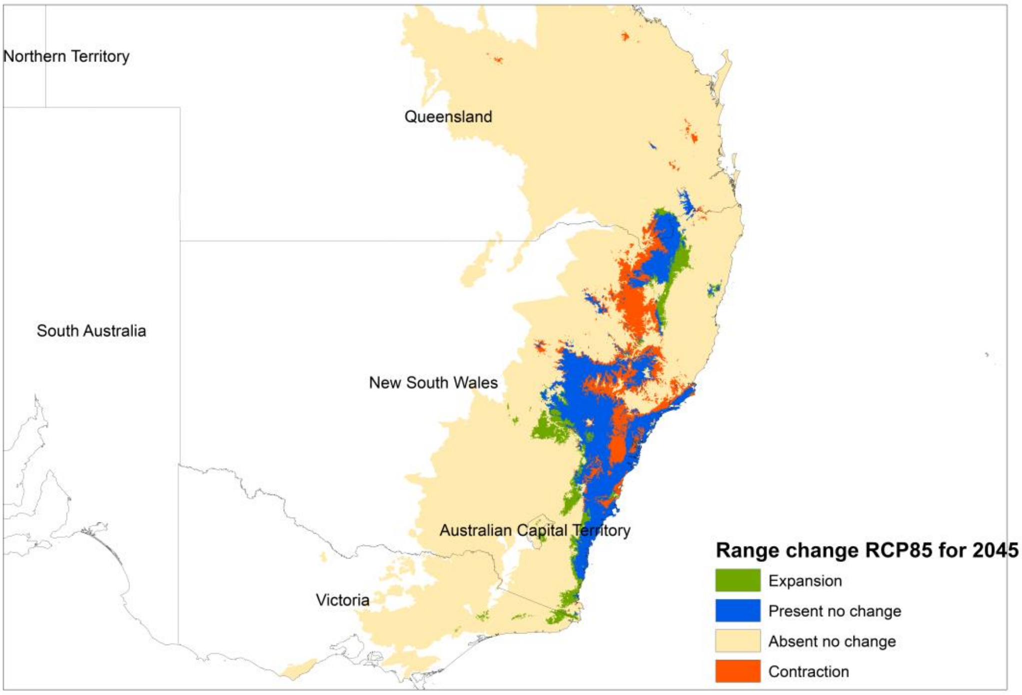

Figure 30. Projected future distribution of the velvet gecko for 2045 under RCP 8.5 emission scenario.

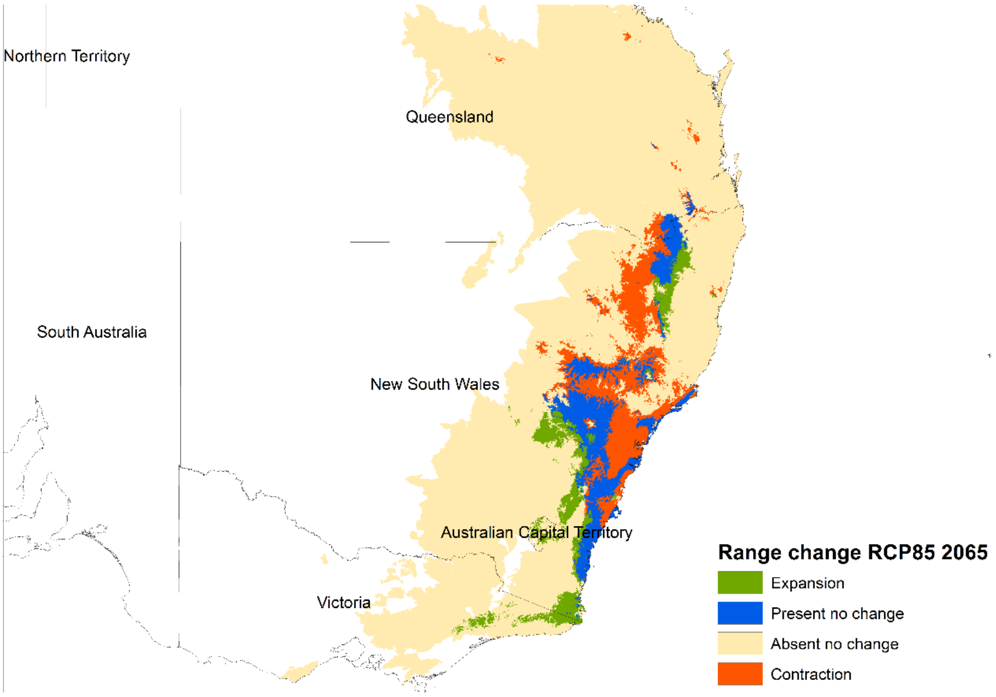

Figure 31. Projected future distribution of the velvet gecko for 2065 under RCP 8.5 emission scenario.

Chapter 4. General Discussion

4.1. Introduction

Habitat destruction and fragmentation are the major threats to biodiversity, but recent studies suggest that climatic change may also pose a serious threat to organisms in coming decades (Leadley *et al.*, 2010). Mean global surface temperatures have risen since 1950, with a rate between 0.113°C and 0.116°C every decade (Karl *et al.*, 2015). If this trend continues unchecked, warming may interact with other threatening processes that affect biodiversity (Parmesan and Yohe, 2003; Parmesan, 2006; Bellard *et al.*, 2012). Rising temperatures may produce range shifts and influence phenology (reviewed in Parmesan, 2006), and could also influence the spread of pathogens (e.g. Lafferty, 2009; Campbell *et al.*, 2015) and invasive species (e.g. Václavík & Meentemeyer, 2012) among others (see Bellard *et al.*, 2012). Changes in climate may also produce range shifts in widely distributed species via dispersal from warm-edges towards the cold-edges (Wiens, 2016; Warren *et al.*, 2018). Understanding how changes in climatic conditions will affect individual species is important for understanding how ecosystems may change as a result of species movements (Lovejoy and Hannah, 2018).

Reptiles are particularly sensitive to climatic changes. Forty percent of reptiles are predicted to lose more than 90% of their range due to climatic change (Warren *et al.*, 2018). Furthermore, most reptiles lack of parental care and have long incubation periods (Shine, 2005), which in turn, leaves the embryos subject to environmental stressors and highlights the importance of maternal nest site choices (Du and Shine, 2015). Incubation temperatures can affect hatching success, and also affect multiple traits in offspring, including sex, size, and performance (Miller, 1985; Van Damme *et al.*, 1992; Gillooly *et al.*, 2001, 2002; Shine and Elphick, 2001; Du and Ji, 2003; Telemeco, Elphick and Shine, 2009; Laloë *et al.*, 2014). In lizards, incubation temperatures can also effect other traits such as physiology, behaviour, spatial learning, and survival of hatchlings (Dayananda *et al.*, 2016; Dayananda and Webb, 2017; Dayananda, Penfold and Webb, 2017; Laloë *et al.*, 2017; Noble, Stenhouse and Schwanz, 2018). Thus, if nest temperatures increase in future, we might see changes in egg hatching success and offspring fitness, which may affect the persistence of local populations.

In this sense, a mother's decision about when and where to oviposit has far reaching effects on maternal and offspring fitness (Bernardo, 1996; Resetarits, 1996). Can females modify their nesting decisions in response to changes in temperature? If so, what features do they adjust to ensure embryo survival or to favour certain offspring phenotypes? How will the geographic range of widely distributed species shift in future? To answer these questions, I studied nest-site selection and modelled range shifts in the widely distributed velvet gecko *Amalosia lesueurii*.

To gauge whether females modify their nesting choices in response to local climatic conditions, I compared thermal and physical traits of nests sites in two populations separated by 250 km. I found that nests from the southern population had a higher percentage of canopy openness and thus of incident solar radiation, than nest from the northern population (Chapter 2). That is, females modified their nesting decisions in response to local climates. This finding mirrors the results of an earlier study on the widely distributed water dragon *Intellagama lesueurii* which found that females selected more open nest sites in colder southern latitudes (Doody, Guarino, Georges, *et al.*, 2006). Perhaps not surprisingly, I found that the mean daily temperatures of velvet gecko nests did not differ between populations. However, the northern population had lower minimum and higher maximum nest temperatures than the southern population. Importantly, there was a significant positive correlation between air temperatures and nest temperatures, so that nests were much hotter during heatwaves. In the northern population, where air temperatures were hotter, nests experienced prolonged periods of thermal stress, suggesting that females in this population could only partially buffer their eggs from the potentially harmful effects of high temperature. These results are similar to a previous study on the eastern three-lined skink *Bassiana duperreyi*, which found that although females nested earlier, and laid deeper nests, the embryos still experienced high temperatures (Telemeco, Elphick and Shine, 2009; Telemeco *et al.*, 2017).

To address how the geographic range of the velvet gecko might shift in future, I used a correlative modelling approach to infer the species current and future distribution (Chapter 3). I then projected for the years 2025, 2045, 2065, and 2085 under the different IPC emission scenarios, and analysed the range shifts in the species. I found that the species current distribution was strongly influenced by the mean temperature of the warmest quarter, which coincides with the species incubation period. Thus, it is possible that environmental temperatures, via their effects on the embryo life stage, define the climatic suitable areas for the species. Modelling showed that geckos will suffer range contractions in future, but some of these contractions would be buffered by southerly range expansions. However, the species occupies highly fragmented landscapes (particularly in the New England Tableland region), and has a poor dispersal ability (Webb, Pike and Shine, 2008), so future range expansions seem unlikely. Like the majority of the Australian reptiles, the major threat to gecko populations is habitat loss and destruction (Webb, Harlow and Pike, 2015). Thus, future climatic models which aim to predict future distributions of lizards must account for the multiple threatening processes that interact to influence their persistence. In addition, future studies should account for how loss of prey may influence predators. In my study, modelling suggested that velvet geckos will disappear from the Sydney Basin bioregion in future. This will have major impacts on the vulnerable broad headed snake *Hoplocephalus bungaroides*. Juveniles of this species feed mostly on velvet geckos (Webb and Shine, 1998), so loss of geckos will likely decrease survivorship of this age class, increasing the risk of local extinctions.

4.2. Future research

My research tackled some important questions, and raised some interesting issues. For example, the lack of parental care in lizards means that females lack confirmation of the success of the previous reproductive event (Refsnider and Janzen, 2010). This lack of information means that females may be unable to adjust their reproductive strategy to cope with rapid changes in the environment. In communally nesting species such as velvet geckos, females may continue to nest in the same locations each year, even though such sites may no longer provide suitable thermal conditions for embryo development. Clearly, we need more information on how females choose nests, and whether they can adjust their decisions to offset rapid changes.

In this respect, the fact that nests of the northern population experienced thermal stress for long periods is concerning. We know that in velvet geckos, higher incubation temperatures can negatively affect hatching success, and can produce smaller offspring (Dayanan*da et al.*, 2016; Dayananda, Penfold and Webb, 2017). However, those studies incubated eggs from the southern population, and it remains possible that embryos from northern populations are more resilient to thermal stress. While there are no such studies on my study species, a recent study on the lizard S*celoporus tristichus* found that exposure to high temperatures (40, 41 or 43°C) for several hours over a 7 day period would cause embryo survival to decline dramatically (Telemeco *et al.*, 2017). To elucidate whether similar effects occur in my study species, future studies should incubate eggs from the northern population under conditions that mimic the temperatures recorded in natural nests from that region.

Although I focused on one aspect of nest-site selection in the velvet gecko, future studies could tackle some other hypotheses for nest-site choice. For example, females might lay eggs in habitats that are optimal not only for egg development and survival, but which are also optimal for hatchling survival (Refsnider and Janzen, 2010; Refsnider *et al.*, 2015). In velvet geckos, females might choose nesting crevices near habitats required by juveniles in order to increase the odds that offspring survive during the dispersal phase from the nest. Such a strategy would decrease the likelihood of predation on offspring. Likewise, laying eggs in communal nests might reduce desiccation of eggs (Radder and Shine, 2007), or might promote synchronous hatching of offspring so as to swamp predators (Doody, Freedberg and Keogh, 2009). Future experiments to test hypotheses about why females choose to lay eggs in communal nests would help to clarify the selective forces that have favoured this strategy.

Finally, I found that precipitation variables play an important role defining the distribution of velvet geckos. How these variables influence each life stage is not understood. Clearly, variation in precipitation may influence prey availability, which in turn may influence reproduction in females. In addition, precipitation may influence the humidity inside nests, which is likely to influence egg hatching success (Packard, Tracy and Roth, 1977; Packard, 1991). Future research examining the influence of temperature and humidity on egg hatching success could help us to understand why precipitation influences the current distribution of the species. Finally, to predict how reptiles will respond to future climatic extremes (droughts and heat waves), we need a better understanding of the sensitivity of the different life stages to thermal and hydric variation (Levy *et al.*, 2015). Research on species like the velvet gecko can provide insights of how climatic changes may affect other lizard species, and can enable us to address current and future threats to ensure that such species survive in future.

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