**Gourret, Arnaud (2016) *The ecology of an arboreal rainforest gecko: Saltuarius cornutus*. MSc thesis, James Cook University.**

# The Ecology of an Arboreal Rainforest gecko: *Saltuarius cornutus*.

Thesis submitted by

**Arnaud Gourret (BSc- Honours)**

October 2016

Thesis submitted in partial fulfilment of the requirements for the Degree of Masters of Science (Research) in the field of Herpetology at the School of Marine Biology and Tropical Biology of James Cook University

**The Northern Leaf-tailed Gecko - *Saltuarius cornutus***

# Abstract

Global temperatures have increased by 0.6°C and are expected to continue rising between 1.4°C and 5.8°C over the next century. In addition to this, recent studies also predict changes in seasonality as well as a higher incidence and rise in intensity of in extreme disturbance events. This unprecedented rate of change in environmental conditions resulting in a loss of biodiversity worldwide raises new questions in conservation: How does one determine a species vulnerability to a changing climate?

Given that their physiology is driven by environmental temperatures, ectotherms are likely to be strongly and directly affected by changes in climate. As a result of their evolutionary history under warm and aseasonal climates, tropical species, in particular, are sensitive to the slightest changes in temperatures. Leaf-tailed geckos (*Saltuarius cornutus)* are cryptic, arboreal geckos occurring in the Wet Tropics rainforests of North Queensland, Australia. I aimed in this study to refine estimates of population size and describe the thermoregulatory ecology of these animals in an attempt to partially measure their exposure to changing environmental conditions.

Due to their cryptic nature and very efficient camouflage, leaf-tailed geckos are very difficult to detect during surveys. As a result, numbers of geckos actually counted are variable and may be inaccurate. As these geckos are arboreal, the main factor affecting their detection is visibility through the canopy. Consequently, in my first chapter I measured the variation in detection probability in relation to canopy height. This, in turn, allowed me to reduce detection bias, and to model occupancy and abundance at various elevations. In contrast to previous estimates, these models revealed a much more homogeneous distribution across the region,

and an even occupancy of leaf-tailed geckos in rainforest habitats at different elevations. In addition, it is likely that a large portion of the population remains undetected in the higher levels of the rainforest canopy, so estimates of abundance are also higher than those made using raw counts.

In the second chapter of this study I aimed to examine some of the behavioral patterns associated with movement and body temperature regulation in these geckos. To do this, I attached thermally sensitive radio transmitters to the animals and remotely recorded their locations and experienced temperatures. In addition to this, I also set up thermal data loggers to monitor air temperature available in the canopy. I found what appeared to be active thermoregulatory behavior. Leaf-tailed geckos seldom moved, and diurnally, were often found in the emergent canopy. Experienced temperatures were significantly higher than surrounding air temperatures, suggesting the animals actively sought warm microhabitats as diurnal retreats. In addition, they remained warmer than air in the evening, suggesting they used tree temperatures to remain warmer than ambient for much of the day, in both winter and summer. Also, the canopy's strongly stratified thermal environments offered cooler and more stable conditions near the ground, where the geckos could potentially find shelter from temperature extremes in future.

In conclusion, the results of this study paint a positive picture with regards to the conservation status of this species. Both parts of the project suggest that these geckos use the canopy's upper levels. Accounting for detection bias in models predicting occupancy and abundance models reinforced the idea that these animals were widespread and abundant in rainforest habitats throughout the region. The results of my behavioral study coincided with this, suggesting geckos preferred the emergent canopy, especially as they seek warmer diurnal

retreats, but also at night. This tendency to thermoregulate, the availability of shelter only a few meters below their present canopy use, and a widespread distribution suggest leaf-tailed geckos populations may have behavioral and habitat options for mitigating the effects of climate change.

# Acknowledgements

I would like to thank my two supervisors Lin Schwarzkopf, and Steve Williams. As the director of the Centre for Tropical Biodiversity and Climate Change, Steve assembled a great team of ecologists who gathered astronomical amounts of environmental and biological data. He is also the one who suggested I study this particular species. I am undoubtedly lucky to have been given the opportunity conduct this research in an environment so rich in both logistical and academic resources. Lin only adds to this with vast knowledge of vertebrate ecology, well-practiced analytical tools and relentless curiosity, traits that give away a candid passion for ecology. Relentless indeed, as she has been my supervisor since I started my Honours in early 2008, and has managed to keep faith in my ability to submit this thesis one day. I cannot overstate the critical role Lin took in pushing me across the finish line.

This research would have never been possible without the old NCCARF grant scheme and the Skyrail Rainforest Foundation grant. This, in addition to a few smaller yet invaluable contributions from more private sources provided all the necessary hardware to gather interesting data in the most unusual ways.

On a more personal note I would like to thank Collin Storlie, Scott Parsons and Jason Schaffer, who in addition to being good friends over the last decade, also provided guidance in all aspects of this study.

Last but not least, to my parents André and Dominique Gourret as well as my partner Véronique Mocellin, thank you for your love and support over all these years. Words fall short to describe how much I appreciate the faith you have placed in me.

# Table of Contents

## List of figures

## List of tables

# Chapter 1. General Introduction.

Global temperatures have already risen by 0.6°C and are expected to increase between 1.4°C and 5.8°C over the next century (Houghton et al. 2001; Root et al. 2003; Williams et al. 2003; Parmesan 2006). This rise in temperature will coincide with increased seasonality in rainfall patterns, as well as a higher incidence of extreme disturbance events such as droughts, floods, storms or cyclones (Houghton et al. 2001; Milly et al. 2002; Williams et al. 2003). Even if organisms have adapted to fluctuating climatic conditions in the past, this unprecedented rate of change is likely to have devastating effects on ecosystems. Additionally, the synergistic effects of anthropogenic environmental changes are predicted to act as catalysts, causing significant reductions in biodiversity (Root et al. 2003). It is already evident that recent climate change is affecting ecosystems across the globe (Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006; Buckley 2008). As a result, it is important for biodiversity conservation to determine which species are most vulnerable to predicted changes in climate (Hughes 2000). Measuring vulnerability requires knowledge of behavioural and physiological traits, in addition to quantified evidence of exposure, sensitivity, resilience and adaptation of species to environmental changes (Williams et al. 2008; Huey et al. 2012).

The Wet Tropics Bioregion (WTB) is the last remaining fragment of tropical rainforest in Australia and a biodiversity hotspot home to at least 65 regionally endemic species (Williams and Pearson 1997). This high biodiversity and endemism is a result of the variation of climatic conditions along orographic gradients creating suitable habitats for a wide variety of rainforest taxa (Williams et al. 2003; Isaac et al. 2009). With changing climatic conditions, species' ranges are expected to shift, expand or disappear (Meynecke 2004; Graham et al. 2005). Model predictions reveal varying degrees of reductions in biodiversity, ranging from local community losses to widespread extinctions due to the disappearance of critical environments, particularly likely for species with limited suitable habitats such as the endemic rainforest obligates of Far North Queensland (Williams et al. 2003; Graham et al. 2005; Isaac et al. 2009).

Ectotherms make up a major part of terrestrial biodiversity, and due to the nature of their physiology, are especially sensitive to changes in temperatures predicted by future climate scenarios (Paaijmans et al. 2013). 'Cold blooded' animals use environmental temperatures to drive metabolic processes, directly linking fitness to the quality of thermal habitats surrounding them (Huey and Kingsolver 1993; Angilletta et al. 2002). Physiological performance of ectotherms can be expressed across environmental temperatures by a right-skewed, bell-shaped curve peaking at a thermal optimum ($T_o$) and declining on either side to reach critical thermal minimum and maximum ($CT_{min}$ and $CT_{max}$ respectively). If exposed to critical temperatures for extended periods of time, physiological processes stop and the animal will die. Aside from these extreme scenarios, suboptimal temperatures reduce physiological performance and fitness, ultimately affecting an organisms' potential for survival within communities (Angilletta et al. 2002).

Evolution under varying climatic regimes causes physiology and performance curves of ectotherms to vary across latitudes (Deutsch et al. 2008). Generally speaking, temperate regions expose species to high variability thermal regimes with temperatures often below thermal optima. As a result, increasing temperatures under future climate scenarios may initially improve their fitness (Deutsch et al. 2008). Additionally, greater physiological plasticity caused by evolution in more variable environments may allow temperate taxa to function in a wider range of temperatures, and to adapt more efficiently to changing conditions. On the other hand, tropical ectotherms have been subjected to warmer and narrower temperature regimes, and are characterised by narrower performance breadths that peak at warmer thermal optima. Consequently, tropical species may be less adaptable to a changing climate, and more susceptible to small shifts in environmental temperatures rapidly reducing fitness (Deutsch et al. 2008). Incidentally, tropical regions also exhibit the highest ectotherm diversity (Kearney et al. 2009).

There are many solutions at all levels of biological organisation to adapt to changing thermal environments (Angilletta et al. 2008). At the smallest temporal scale, ectotherms control body temperature behaviourally by adopting postures and shuttling between microhabitats with particular thermal qualities. Behavioural thermoregulation is, therefore, vital to maintain optimal performance (Huey and Kingsolver 1993; Angilletta et al. 2002). As mentioned above, temperate ectotherms generally experience lower temperatures and thermoregulation is typically aimed at increasing body temperatures. In contrast to this, tropical ectotherms already experience environments close to if not exceeding thermal optima, causing behaviours designed to keep them from overheating (Kearney et al. 2009). As a result, a thermally heterogeneous habitat matrix is often key to provide opportunities to adjust body temperature, and understanding patterns in environmental temperatures, as well as the extent to which ectotherms use them, is therefore crucial (Paaijmans et al. 2013). Tropical rainforest canopies offer a wide range of microhabitats that influence local biodiversity patterns from the rainforest floor to the emergent canopy (Fletcher et al. 1985;

Scheffers et al. 2013). In addition to this, vertical stratification in the rainforest also creates the widest thermal gradient, making arboreality the most advantageous strategy for thermoregulation (Scheffers et al. 2013).

My study focuses on refining estimates of population size and describing the thermoregulatory ecology of a tropical arboreal ectotherm, the northern leaf-tailed gecko, *Saltuarius cornutus*, thus contributing to our understanding of its exposure and therefore vulnerability to climate change. Repeated surveys over the last 20 years allowed me to calculate the detectability of these geckos and estimate more accurately the occupancy and abundance of individuals. Additionally, to describe canopy temperatures and stratification, air temperatures were recorded at varying heights in rainforest canopies across the mountain ranges of the Wet Tropics, providing a detailed record of temperature fluctuations across latitudes, elevations and seasons. Subsequently, this apparatus was re-located to record canopy temperatures at one particular site at high resolution, offering a more detailed picture of air temperatures in the canopy, and allowing me to compare available environmental temperatures with remotely gathered information on movement and experienced temperatures recorded by thermally sensitive transmitters attached to wild, active *S. cornutus*.

This thesis was structured into 2 data chapters: CHAPTER 2 examined the detection probability of northern leaf-tailed geckos (*S. cornutus*) in standardised surveys, allowing me to make estimates of the size of the undetected portion of the population at the sites, providing better estimates of occupancy and abundance across relevant environmental gradients. CHAPTER 3 compared the distribution of environmental air temperatures available for thermoregulation and those experienced by the geckos. This, in turn, allowed me to determine how actively leaf-tailed geckos regulate their body temperatures and what part of the canopies' thermal stratification they use, evaluating the potential for buffering detrimental temperatures through vertical movement.

# Chapter 2. Estimates of occupancy and abundance for a cryptic arboreal gecko.

## 2.1 Introduction

Estimating wildlife population size over time and space has always been a major focus of ecological studies (MacKenzie et al. 2002; Yoccoz et al. 2001). Such estimates, however, are influenced by sampling design, environmental factors, and the behaviour and appearance of the target species (O'Connell et al. 2006). It is naïve to assume that all individuals of a population will be detected during surveys, so raw counts provide biased underestimates of abundance (Yoccoz et al. 2001). Measures of population size are affected by two main sources of variability: first the true distribution of individuals across the range of available habitats, and secondly, variation in detection probability in different habitats and under different environmental conditions (MacKenzie et al. 2002; Yoccoz et al. 2001). It is, therefore, important to design sampling protocols and analyses that enable us to quantify the abundance of a target species while accounting for detection probability, to describe true variations in abundance.

Cryptic species, by their very nature, are difficult to detect, making it especially hard to estimate their abundance (MacKenzie et al. 2002). Northern leaf-tailed geckos, (*Saltuarius cornutus*) are nocturnal, arboreal and highly cryptic because they have particularly efficient camouflage (pers obs.), and therefore, estimation of their population sizes can be difficult. A family of statistical models has been developed and tested to predict either occupancy or abundance from count data. Such models allow us to more accurately describe species distributional patterns (MacKenzie et al. 2002, Royle and Nichols 2003, He and Gaston 2003), because they account for imperfect detection, addressing bias (Kery 2011).

This study aimed to estimate occupancy and abundance of northern leaf-tailed geckos. We used these estimates to describe patterns of habitat use by this species in relation to canopy height and elevation, while accounting for detection bias caused by visibility through the canopy.

## 2.2 Materials and methods

*Saltuarius cornutus* is a cryptic arboreal gecko, restricted to mountainous rainforests, and endemic to the Wet Tropics Bioregion of North Queensland, Australia. In addition to a nocturnal habit, efficient camouflage makes it difficult to distinguish from the bark, moss and lichen on which it typically resides. Although they are difficult to find, and as part of wider studies of vertebrate species patterns, populations of northern leaf-tailed geckos were surveyed repeatedly for 9 years in a variety of habitat patches at a range of elevations, and in two seasons (wet and dry) in the Wet Tropics Bioregion of North Queensland, Australia. I used observations of *Saltuarius cornutus* gathered over 298 spotlighting surveys performed between 2005 and 2013 at 40 sites across latitudinal and elevational gradients between Townsville and Cooktown from sea level to 1500 above sea level, in closed rainforest (Webb and Tracey 1994). Prior to each hour long, 1-km survey, trained surveyors recorded environmental variables relevant to the detection and activity of the target species (air temperature in °C and relative humidity, as well as indices of cloud, rain, substrate wetness, wind, mist and moonlight). For each gecko located, an approximate height in the canopy was also recorded.

The occupancy and abundance models were built as described in Mackenzie et al. (2002 and 2003) and implemented in the *R* Statistical Software Package v. 2.15.1 (*R* Core Team 2012) using the package ‘unmarked’ (Fiske *et al.* 2012). Combinations of the above variables were tested to measure potentially significant effects on detection probability, to create refined estimates of occupancy across elevational gradients.

Canopy strata were divided into 6 categories (0-5m, 5-10m, 10-15m, 15-20m and 20 to 25m, and 25-30m), and 6 models were fitted to the data: a null model with no covariates, and 5 others using elevation as a covariate for occupancy or abundance (Ψ) and cycling through combinations of covariates (canopy height, air temperature, wind and years) to estimate detection probability (p). All 6 formulae were used to estimate both occupancy and abundance using the relevant functions, but predictions of detection probability were made based on the best-fitting model.

The goodness of fit of predictions of detection were quantified with a Pearson’s Chi-squared statistic, comparing observed and predicted numbers of geckos across canopy heights for both occupancy and abundance in different seasons (MacKenzie and Bailey 2004). I then compared models with different covariates using Akaike’s Information Criterion (AIC), using ΔAICs and AIC weights highlighting the most efficient models to estimate occupancy or abundance. Finally, I calculated naïve estimates of abundance and occupancy, excluding any measure of detectability, and measured the difference between those and adjusted predictions.

## 2.3 Results

Height in the canopy and air temperature were the best predictors of detection probability for both occupancy and abundance (Table 2.3.1.).

Table 2.3.1. Statistics and ranking for model selection. Formulae shown here express the covariates used for detection (p), and the covariates used to predict occupancy or abundance (Ψ).

| Model | Formula | Ψ | SE(Ψ) | nPars | AIC | Δ AIC | AICwt | C-wt |
|---|---|---|---|---|---|---|---|---|
| Occupancy | p(Height) Ψ(Elevation) | 0.000416 | 0.000659 | 4 | 1528.62 | 0 | 5.60E-01 | 0.56 |
| | p(Height + Air-T) Ψ(Elevation) | 0.000517 | 0.000674 | 5 | 1530.73 | 2.1 | 2.00E-01 | 0.75 |
| | p(Height + Wind) Ψ(Elevation) | 0.000639 | 0.00066 | 5 | 1530.84 | 2.22 | 1.80E-01 | 0.94 |
| | p(Height + Air-T + Wind) Ψ(Elevation) | 0.000677 | 0.000668 | 6 | 1533.04 | 4.42 | 6.10E-02 | 1 |
| | p(·) Ψ(·) | -0.337 | 0.159 | 2 | 1605.39 | 76.77 | 1.20E-17 | 1 |
| | p(Height + Air-T + Wind + Year) Ψ(Elevation) | -5.01E-05 | 0.000619 | 7 | 1621.55 | 92.92 | 3.70E-21 | 1 |
| Abundance | p(Height + Air-T) Ψ(Elevation) | -0.000167 | 0.000226 | 5 | 1515.37 | 0 | 4.30E-01 | 0.43 |
| | p(Height) Ψ(Elevation) | -0.000222 | 0.00021 | 4 | 1515.82 | 0.45 | 3.40E-01 | 0.78 |
| | p(Height + Wind) Ψ(Elevation) | 2.87E-05 | 0.000216 | 5 | 1516.93 | 1.56 | 2.00E-01 | 0.97 |
| | p(Height + Air-T + Wind) Ψ(Elevation) | -0.000213 | 0.000231 | 6 | 1521.02 | 5.65 | 2.60E-02 | 1 |
| | p(Height + Air-T + Wind + Year) Ψ(Elevation) | 0.000205 | 0.000224 | 7 | 1548.23 | 32.86 | 3.20E-08 | 1 |
| | p(·) Ψ(·) | -0.46 | 0.131 | 2 | 1577.21 | 61.85 | 1.60E-14 | 1 |

The model predicting occupancy found that detectability decreased significantly with increasing height in the canopy (Fig 2.3.1.). Standard errors remained constant from 0 to 30 m in the canopy. In contrast to this, the model predicting abundance found that detectability was influenced by both height in the canopy and air temperature (Fig 2.3.2.).

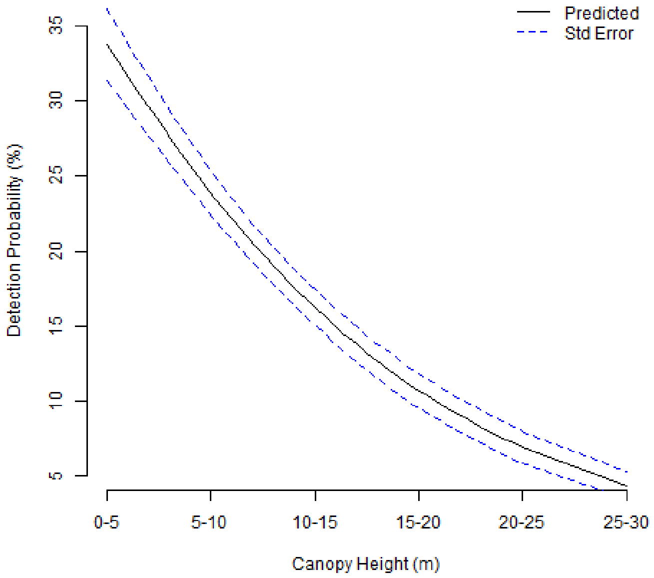


Fig 2.3.1. Using occupancy, predicted detection probability of *Saltuarius cornutus* across canopy heights during biodiversity surveys.

Models using abundance predicted a slightly lower probability of detection in relation to canopy height than models using occupancy, and a considerably greater error rate near the ground, which decreased with lower detection probabilities higher in the emergent parts of the canopy. Lower temperature also slightly reduced detection probability when abundance was predicted.

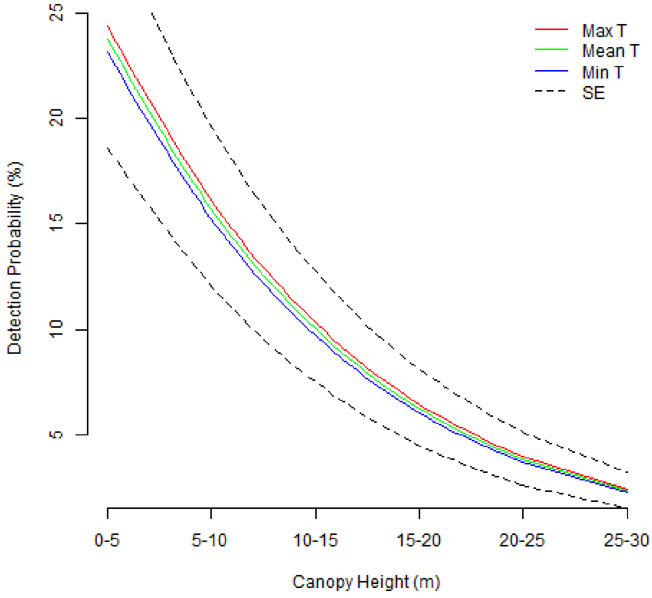


Fig 2.3.2 Detection probability of *Saltuarius cornutus* as predicted using abundance, with height in the canopy and air temperature as covariates.

For both occupancy and abundance models, models using elevation fit the empirical data better than null models (Table 1). Predicted occupancy increased slightly with elevation with a very weak positive coefficient (Table 1 & Fig 3). Occupancy was more or less constant (approximately 44% occupancy at all sites) over the elevational gradient. In contrast to that, estimates derived directly from raw observations varied widely, and in many cases were considerably greater than those estimated by the model, with the highest rates of occupancy at both extremes of the elevational gradient. Estimates of abundance mirrored those of occupancy, with a very weak negative relationship with elevation (Table 1 & Fig 4). Abundance estimates also stayed constant from sea level to mountain peak, with a small decrease at high elevations. Observed estimates of abundance were less erratic than those of occupancy in Fig 3, with a normal distribution over elevations. Estimates of detectability fit the data well (non-significant $X^2 = 20$, df = 16, $p > 0.05$; MacKenzie and Bailey 2004).

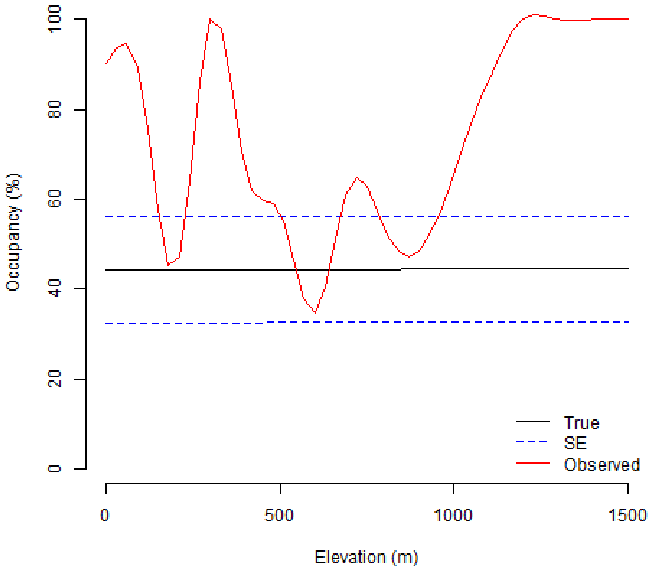


Fig 2.3.3 Predictions of occupancy modelled across elevations using detection probability to re-calibrate estimates initially calculated directly from observed values.

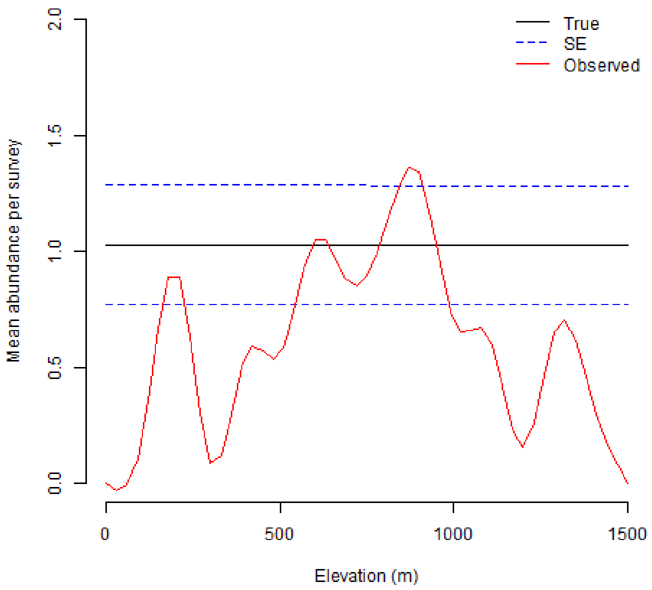


Fig 2.3.4 Predictions of abundance modelled across elevations using detection probability to re-calibrate estimates initially calculated directly from observed values.

## 2.4 Discussion

Northern leaf-tailed geckos are highly cryptic, arboreal lizards, and therefore visibility through the canopy is an important obstacle to detection during surveys; an impediment exacerbated by dense rainforest vegetation and the species' nocturnal habit. Appropriately, therefore, we found that detection rates were significantly affected by canopy height, such that geckos higher in the canopy are harder to detect (Figs 1 & 2). Temperature also influenced detectability because geckos are ectotherms, and are therefore less likely to be active when temperatures are lower (Fig 2.). Overall, a lower detection rate was predicted by the model predicting abundance (Royle and Nichols 2003), than by the model predicting occupancy (MacKenzie et al. 2003). The difference in the predictions of the two models probably occurred because the probability of correctly estimating abundance is lower than the probability of detecting the presence of any individual in a population. We also found that while a better fit is achieved by models using elevation to predict occupancy or abundance, both estimates remained constant from 0 to 1500 m, suggesting the geckos are likely to be more evenly spread throughout this topographical gradient than it appears from raw counts.

For conservation, it is important to determine whether animals are rare, or just difficult to detect. Our estimates of occupancy and abundance were somewhat sensitive to changes in detectability, but the models predicted an approximately constant presence of northern leaf-tailed geckos across elevations. Difficulties detecting geckos above 10 m in the canopy meant that surveys typically missed a large proportion of the population in the upper canopy, and as a result, the abundance model estimated a population size 60% greater than that estimated by raw counts. Predicted occupancy, however, was reduced compared to naïve occupancy, which reached 100% at some of the sites where detection was not strongly limited.

Using accurate measures of detection probability is central to avoiding biased estimates of both occupancy and abundance, particularly for cryptic and nocturnal species like *S. cornutus*. Similar methods have helped refine population size estimates for a variety of taxa subject to detection bias, from multispecies models depicting amphibian occupancy to regional estimates for rare or migratory birds (MacKenzie et al. 2002; MacKenzie and Kendall 2002; MacKenzie et al. 2003). Estimates of detectability can vary greatly across relevant gradients, even within taxonomic groups (this study; Magurran and Henderson 2003; Durso et al. 2011). Reducing detection biases allows us to pinpoint the habitat requirements most important to the occurrence of rare species (Roughton and Seddon 2006; Blevins and With 2011). This analysis also allows researchers to evaluate the efficiency of various sampling methods for different target species, and to define the main sources of variability in detection probability. Generally, removing detection biases reduces unexplainable variation in estimates of population sizes, however precision in estimates can be reduced by very low detection probabilities (<0.5%). In most instances, using detection probabilities produces very different estimates of occurrence, and the new estimates are less variable and more ecologically relevant (Bailey et al. 2004; MacKenzie et al. 2005; O'Connel et al. 2006; Mazerolle et al. 2007). Finally, this method of estimating detectability and population size is practical, as it requires only presence-absence counts, which are available even with limited resources (time, effort and funding) in contrast to other methods such as mark-recapture studies (Mazerolle et al. 2007). Our models demonstrate that observations made over the past 9 years reveal only a fraction of the population likely to be present at those sites. I provide here a simple but sound estimate of abundance with which comparisons can be made in the future. A similar analysis using different state variables could be used to examine the effects of various environmental parameters or impacts on population size (using state covariates such as habitat patch size and stability, or time). It is, however, clear that the use of canopy height to measure detection probability was successful in removing some observer biases, allowing for a more realistic description of the densities of leaf-tailed geckos.

# Chapter 3. Evidence for thermoregulation in a thermoconformer: the behaviour and habitat use of a rainforest gecko.

## 3.1 Introduction

The most common and effective way for medium-sized ectotherms to regulate their body temperature is by behaviourally selecting appropriate temperatures from available spatial thermal heterogeneity (Deutsch et al. 2008; Kearney et al. 2009; Aubret and Shine 2010), although physiological and morphological adaptations may help buffer the effects of environmental temperatures on ectotherms (Angilletta et al. 2006). Temperate species generally experience environmental temperatures lower than their thermal optima, and therefore choose habitats to raise body temperatures ($T_b$). In contrast to this, shade and cooler refugia may be more important for tropical ectotherms exposed to considerably warmer temperatures (Kearney et al. 2009, Vickers et al. 2011). Avoiding, rather than gaining heat is therefore the main concern for many tropical ectotherms (Huey et al. 2009; Kearney et al. 2009; Kingsolver 2009; Vickers et al 2011).

Behavioural thermoregulation in nocturnal lizards is particularly interesting as they are usually active at the coolest and most thermally homogeneous part of the day. Nocturnal lizards' (e.g., geckos') body temperatures during the daytime are often comparable to those of diurnal lizards, suggesting that they may thermoregulate during the day (Angilletta et al.

1999; Angilletta and Werner 1998). Nocturnal activity may allow predator avoidance, increased foraging success or reduced costs of maintenance, while diurnal thermoregulation maintains the animal near optimal temperatures to conduct metabolically demanding processes such as digestion and growth, while not moving much (Autumn and DeNardo 1995; Angilletta et al. 1999; Kearney and Predavec 2000; Weeks and Espinoza 2013). Studies focusing on nocturnal lizard activity during the day have observed individuals choosing considerably hotter retreats than randomly found in their surroundings, and adopting specific postures to maximize interactions with desired environmental temperatures, hence achieving significantly warmer body temperatures (Angilletta et al. 1999; Kearney and Predavec 2000; Kearney 2001).

The diurnal behaviour of geckos living in tropical rainforests is especially interesting, as this type of closed forest is famous for its low thermal heterogeneity, and for the unusual, thermoconforming behaviour of many of the lizards that occupy it (Huey 2009). Given the possible lack of thermal heterogeneity available in the day in rainforests, it is interesting to determine whether rainforest geckos can thermoregulate diurnally. Rainforest geckos, presumably already adapted to activity in low thermal heterogeneity environments and living in warm, tropical rainforests, seem especially likely to be thermoconformers.

I described the daily and seasonal air temperature gradients available in rainforest canopies and quantified body temperatures selected by active northern leaf-tailed geckos, *Saltuarius cornutus* in their natural environment of closed canopy rainforest, comparing both datasets searching to determine if these geckos might thermoregulate.

## 3.2 Materials and Methods

### *3.2.1 Recording environmental parameters.*

This study was conducted at 700m elevation on Mt Edith, SW of Cairns, in Tropical North Queensland, Australia. I recorded shaded air temperatures every hour between March 2013 and May 2014, using 4 sets of thermal dataloggers (Thermochron iButtons$^{TM}$) attached to trees from 4-m above the ground to as high as possible in the emergent canopy (iButtons were placed every 3 meters to 16, 19, or 22 meters above the ground, depending on the height of the canopy). iButtons, sheltered from direct sunlight and weather by large (40cm W x 12cm H), opaque, white plastic cones and placed in a spherical metal mesh sieve (a tea strainer), were attached to a galvanised steel chain, anchored to the ground and attached to a branch at the top of the tree.

All iButtons were calibrated using water baths at 5°C intervals between 10°C and 30°C. Water temperatures were kept constant (confirmed using a calibrated mercury thermometer [Brannan$^{TM}$ Immersion in-glass]), and the iButtons$^{TM}$ recorded temperatures every 2 minutes. Both water bath and recorded temperatures were plotted, and a linear relationship was determined for each logger, providing the correction (if any) that needed to be applied to the data, once environmental temperatures were downloaded from the loggers.

### *3.2.2 Radiotracking*

I fitted 3 Northern Leaf-tailed geckos (*Saltuarius cornutus*) with factory calibrated, thermally sensitive radio-transmitters (Holohil Systems BD-2N), attached to silicone capillary tubing over two tracking sessions in August 2013 and January 2014. These harnesses were tied with cotton thread and attached like a belt around the inguinal region

(Gourret et al. 2011). Geckos were released within 24 hours of capture and repeated observations made at 3-hourly intervals (from 6:00 to 12:00) until the transmitter signal stopped (up to 5 days). For each observation, I recorded characteristics of habitat use as well as the number of transmitter pulses emitted over three minutes, as a measure of temperature.

To describe habitat use, I recorded height in the canopy (meters), compass orientation, substrate use (on tree trunks, in moss, on vines, on tree limbs, in tree canopy), as well as air and substrate temperature (at ground level) with a glass mercury thermometer and IR thermometer (Fluke, 62 Mini IR thermometer) respectively. Because visibility is limited in rainforest canopies, orientation and height of the geckos were sometimes estimated using the directionality of the Yagi antenna and the strength of the signal received: orientation was determined by moving around the tree and stopping at the strongest signal, and height by moving away from the base of the tree in that same direction and determining the angle from vertical of the strongest signal, and estimating the height from that trajectory.

### *3.2.3 Statistical methods*

To describe fluctuations of environmental temperatures, environmental air temperatures were averaged over daily and seasonal cycles and plotted over time. In addition, the effect of canopy height on air temperature was described using linear regressions for both winter and summer. I used the environmental canopy temperatures collected during tracking sessions at both locations and times. I then compared various combinations of air and radiotransmitter temperatures using Kolmogorov-Smirnov tests. Finally, radiotransmitter temperatures and observed height in the canopy for each gecko were compared to available environmental temperatures at those heights to determine the relationship between habitat air temperatures and temperatures selected by the geckos.

## 3.3 Results:

### *3.3.1 Environmental temperatures*

Overall mean temperatures at all heights and sites decreased from summer to winter. More interestingly, on a daily scale, temperatures increased and stratified during the day and homogenised at night. The stratification was strongest during the day, with the highest data loggers recording the largest difference from the ground temperatures (Fig 1 A & B). Air temperatures at 4-7 m increased more slowly and reached lower maxima than those higher in the canopy. The relationship between mean temperatures and height in the canopy also varied seasonally, with the thermal stratification increasing in winter.

### *3.3.2 Movement of S. cornutus in the canopy*

In the day, leaf-tailed geckos spent 100% of their time in the emergent canopy. Geckos were only visible in the sub-canopy late at night (23:00), and were out of sight and back in the emergent canopy by the first observation at 6:00. Correspondingly, we suspect that geckos spent most of their time on limbs amongst the foliage of the canopy, coming down on the trunk at night when foraging (all observed geckos exhibited this behaviour, though varying in extent, moving between 3 to 5 meters vertically), where we could observe them directly. On average, geckos moved no more than 5 meters over their daily cycle, and remained above 10m at all times (Figures 2 & 3).

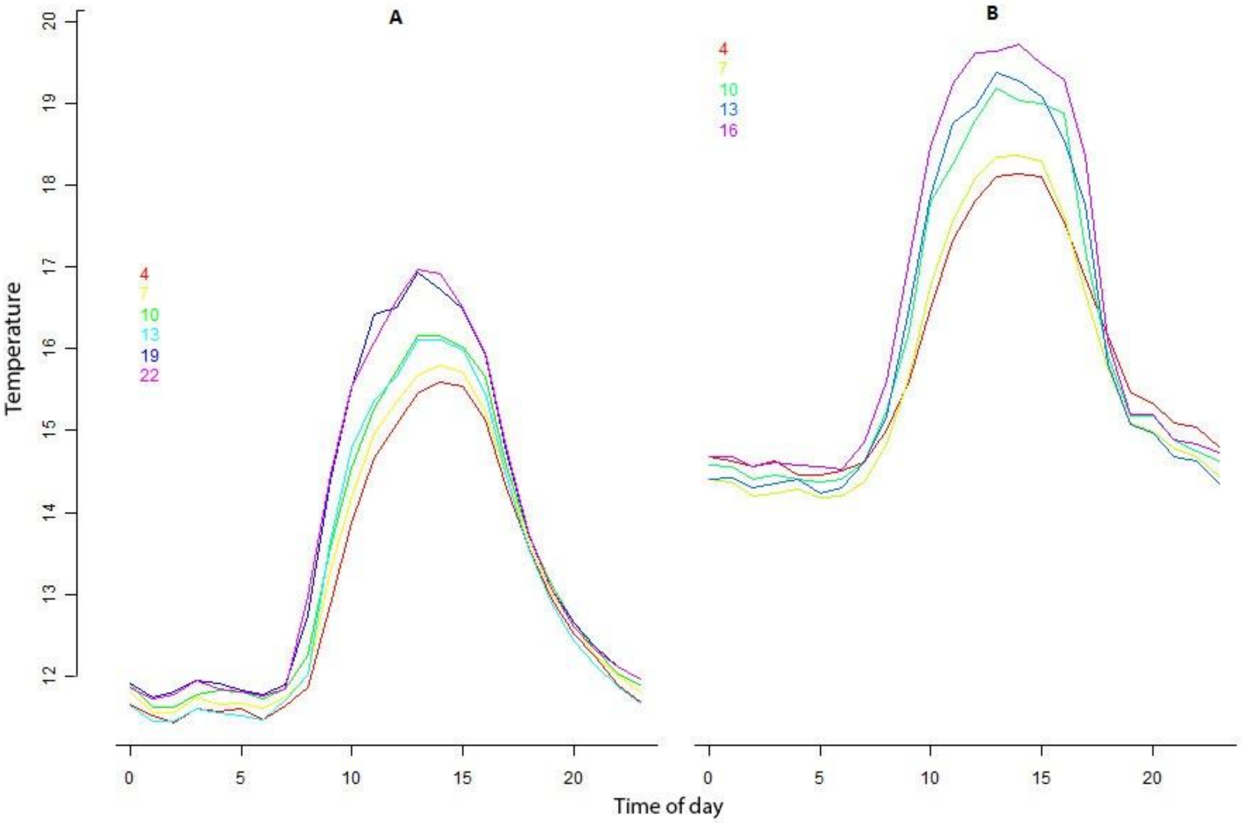


Fig 3.3.1 Daily variation in mean canopy air temperatures. Colours express different canopy heights, and temperatures reported by the curves are hourly averages at individual heights. 1A shows the temperatures found in Carbine Uplands (1200m) in winter (July 2013)and 1B the Lamb Range Uplands (900m elevation) in summer (February 2013).

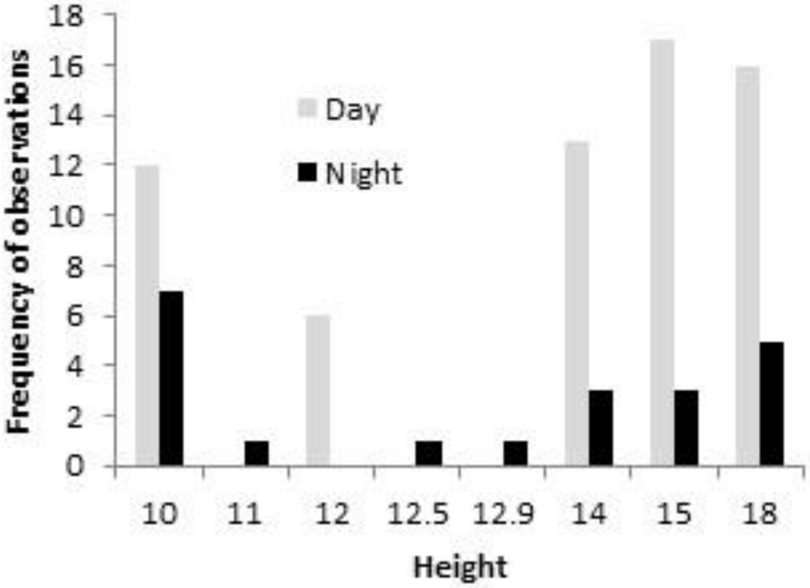


Fig 3.3.2 Height use observed during radiotracking. Geckos (*Saltuarius cornutus*) remained in the sub-canopy to emergent canopy, with preference for higher positions diurnally.

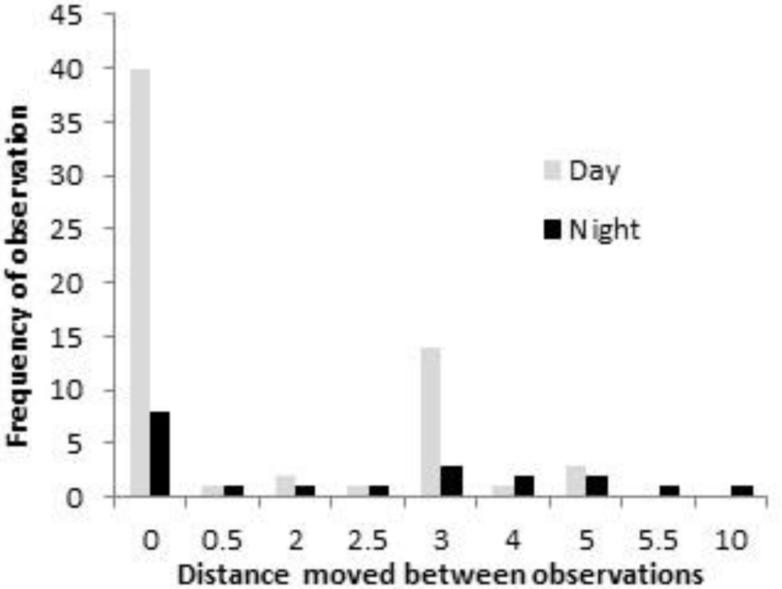


Fig 3.3.3 Distance moved between observations. Most of the time geckos moved very short distances (90 observations).

### *3.3.3 Thermoregulation*

Geckos were significantly cooler at night than in the day in both seasons (Kolmogorov-Smirnov test, $p < 0.006$ in both seasons), but not significantly cooler in winter than summer (K-S test, $p > 0.006$). In addition to this, transmitter temperatures were significantly higher than air temperature in both seasons, sometimes by up to 15°C (K-S test, $p < 0.0001$ in both summer and winter). Finally, transmitter temperatures were always significantly warmer than air temperatures both diurnally and nocturnally over winter and summer (K-S test, $p < 0.006$ for diurnal summer, for nocturnal summer, for diurnal winter, and for nocturnal winter; Table 1. & Fig 4.).

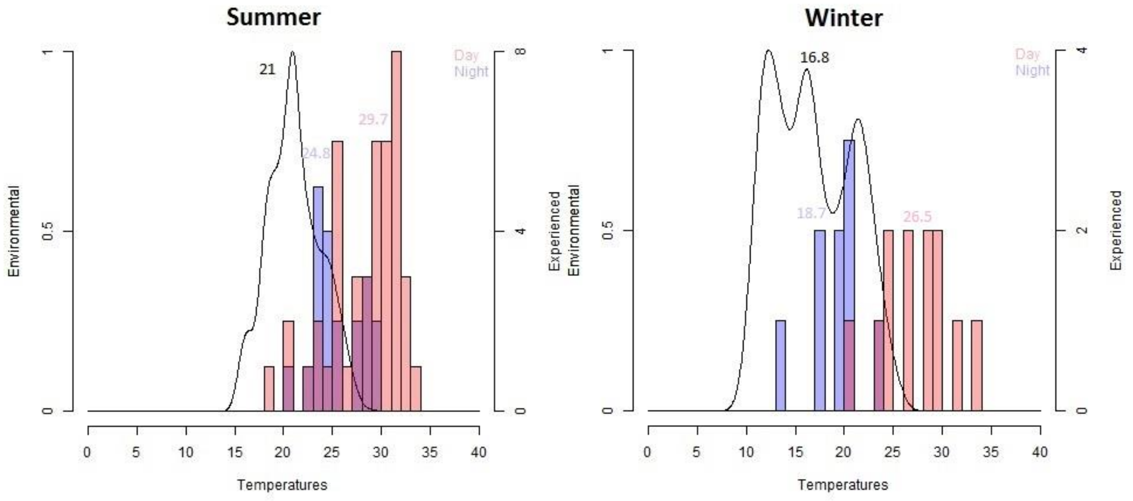
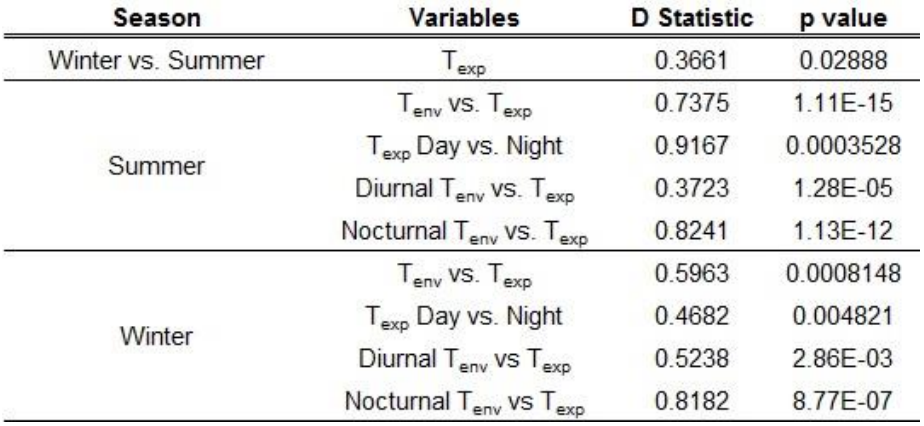


Fig 3.3.4 Temperatures experienced nocturnally and diurnally in relation to recorded $T_{air}$ in both the summer (left) and winter (right). The black line represents the air temperatures in the canopy and means are shown above the corresponding distributions.

A comparison between radiotransmitter and air temperatures at the same estimated height and at the time of observation of radiotransmitter temperatures shows that radiotransmitter temperatures were frequently above the maximum thermal envelope recorded by the data loggers (Fig 5.).

Table 3.3.1 Results of Kolmogorov-Smirnov tests comparing environmental and experienced temperatures over seasons and daily cycles, the temperature distributions of which are shown in Figure 5.



| **Season** | **Variables** | **D Statistic** | **p value** |
|---|---|---|---|
| Winter vs. Summer | $T_{exp}$ | 0.3661 | 0.02888 |
| Summer | $T_{env}$ vs. $T_{exp}$ | 0.7375 | 1.11E-15 |
| | $T_{exp}$ Day vs. Night | 0.9167 | 0.0003528 |
| | Diurnal $T_{env}$ vs. $T_{exp}$ | 0.3723 | 1.28E-05 |
| | Nocturnal $T_{env}$ vs. $T_{exp}$ | 0.8241 | 1.13E-12 |
| Winter | $T_{env}$ vs. $T_{exp}$ | 0.5963 | 0.0008148 |
| | $T_{exp}$ Day vs. Night | 0.4682 | 0.004821 |
| | Diurnal $T_{env}$ vs $T_{exp}$ | 0.5238 | 2.86E-03 |
| | Nocturnal $T_{env}$ vs $T_{exp}$ | 0.8182 | 8.77E-07 |

Thus, *Saltuarius cornutus* appears to choose locations high in the canopy during the day and often experienced temperatures 6-8°C higher than data loggers suspended at the same height.

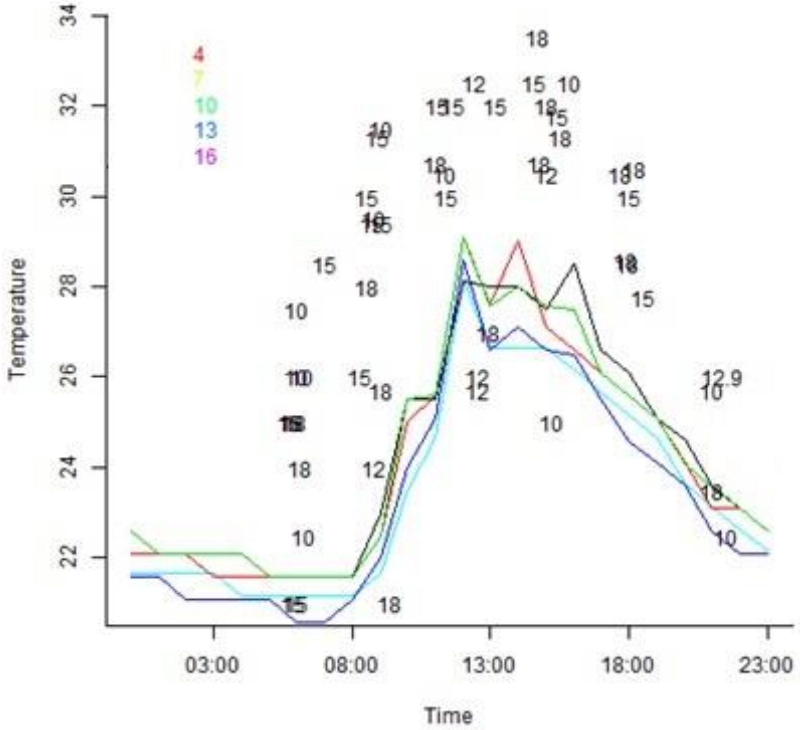


Fig 3.3.5 Comparison between maximum temperatures recorded by shaded data loggers positioned at various heights in a rainforest canopy (colored lines), and the body temperatures of *S. cornutus* at similar heights in January 2014. Numbers indicate the estimated height for each observation.

## 3.4 Discussion.

The thermal environment (measured by air temperature) available to northern leaf-tailed geckos (*Saltuarius cornutus*) in rainforest canopies was surprisingly variable, contrasting with the widespread image of rainforest environments as highly thermally stable (Shaw et al. 1988; Davies-Colley et al. 2010). Thermal stability increased from the emergent parts of the canopy to the ground, and temperatures at all elevations and heights decreased seasonally from summer to winter, and throughout the day from photophase to scotophase, respectively. In addition, there was strong diurnal stratification of temperatures across canopy heights: dawn was marked by an increase in the range of temperatures from the top to ground level in the rainforest (Fig 1.). Because temperatures in the canopy were more stratified during the day, there was a wider range of thermoregulatory opportunities for these geckos diurnally than nocturnally. Seasonally, the relationship between height and temperature became more pronounced during the winter, further increasing the spread of temperatures across canopy layers and, as a result, also increasing the potential for thermoregulation even if overall temperatures were lower.

The thermal quality of diurnal retreats is very important for the fitness and survival of many nocturnal reptiles (Aguilar and Cruz 2010; Webb and Shine 2000). Radiotracking data indicated that northern leaf tail geckos often occupied the higher parts of the canopy, and transmitter temperatures were almost always higher than recorded air temperatures. While we might expect gecko body temperatures (and radiotransmitter temperatures) to differ from air temperatures by several degrees, due either to heating from direct solar radiation and thermal hysteresis, or both, we noted large differences (up to 6°C, mean 3.5°C) between radiotransmitter and air temperatures, suggestive of behavioural activity by the geckos to raise body temperature. Direct solar radiation can cause strong thermal differences between air and object temperatures, and decreases from the top to the bottom of the canopy. The effects of direct radiation on object temperatures in this environment is therefore more likely to occur towards the emergent canopy, suggesting that the major influence on radiotransmitter temperatures may well have been the use of the emergent canopy by the geckos.  Temperatures recorded by the radiotransmitters differed significantly from environmental air temperatures recorded by the data loggers at the same height in both seasons (Fig 4, Table 1). Because data loggers monitored shaded air temperature at predetermined heights, it is reasonable to cautiously suggest that at least part of the higher temperatures achieved by *Saltuarius cornutus* were the result of behavioural choices and habitat use.

In contrast to daytime observations, nocturnal radiotransmitter temperatures were closer to, but still deviated from, maximum air temperatures in the canopy. Depending on bark type and colour, and the intensity of solar radiation received, trees can retain heat several hours after sundown, particularly in a humid and warm environment such as a tropical rainforest canopy (Coombs et al. 2010, Nicolai 1986). In addition to that, morphology and the postures adopted by leaf-tails may maximize contact with the substrate and reduce wind exposure, allowing experienced temperatures to stay closer to substrate temperatures and considerably warmer than those recorded by our data loggers hanging in the canopy. The potential use of hollows and crevices as retreat sites would result in even greater differences between air and experienced temperatures (Pinowski et al. 2006).

On some occasions, geckos were seen moving low in the canopy at night, but they always moved back to locations high in the canopy in the morning. Geckos are usually nocturnal, using low temperatures and reduced thermoregulatory opportunities at night to move and forage with lower energy expenditures, and diurnal inactivity in a chosen retreat to boost other physiological processes (Angilletta et al. 1999; Autumn and DeNardo 1995). The patterns in Figures 4 & 5 are consistent with this behaviour. Diurnally, *Saltuarius cornutus* occupied the highest canopy layers, maybe to take advantage of warmer temperatures in the areas of the canopy reached by solar radiation. However, as a nocturnal, high-elevation species, northern leaf-tails are comfortable foraging when a large part of their habitat is cool: i.e., at night when gradients are minimal and mean canopy temperatures lower, costing them less energy (Hare et al. 2007; Autumn et al. 1997). Leaf-tails spend less time at the top of the canopy at night, probably because the thermal gradient available for thermoregulation is reduced, and other factors, such as foraging success, may determine activity location. Active diurnal thermoregulatory behaviour has been observed in other nocturnal ectotherms (Kearney and Predavec 2000; Kearney 2001) and is, indeed, thought to be due to a separation of tasks by lizards in which locomotion and foraging are not inhibited by lower night time temperatures, but higher diurnal temperatures are still used to increase the lizard's metabolism (Aguilar and Cruz 2010).

In addition to a more active diurnal thermoregulatory behaviour than previously thought, *Saltuarius cornutus* may benefit from the cooler and more stable thermal habitat found closer to the rainforest floor. The buffering qualities of the rainforest canopy create the steepest thermal gradient available on the smallest possible scale (Scheffer et al. 2013). This steep gradient of temperatures may, in turn, shelter the animals from particularly high extremes in temperatures, which could cause reduced fitness, if not death (Vickers et al. 2011).

Our study provides an interesting hint that these large rainforest geckos may not be thermoconformers, but may make use of the thermal heterogeneity available in the emergent canopy to thermoregulate diurnally. Future studies could confirm this by, first examining thermal selection by these geckos in a thermal gradient, to determine if they do seek out warmer microhabitats during the day. Secondly, thermal models designed to determine operative environmental temperatures available to these lizards (e.g., Huey 1982) should be deployed in the canopy, to directly quantify the temperatures that would be experienced by these geckos in these locations, and provide a better measure of available thermal environments than air temperatures.

# Chapter 4. General Discussion.

Suitable conservation solutions can only be determined by investigating a species' vulnerability, as ensuing from interacting exposure and sensitivity to various stressors. The latter is expressed through adaptive capacity and resilience, as a result of synergy between the organism’s ecology, physiology and genetic diversity (Williams et al. 2008). This study focuses on defining the distribution and behavioural ecology of *Saltuarius cornutus*, particularly the gecko’s use of canopy microhabitats in potentially buffering its exposure and inherently affecting vulnerability to a changing climate.

## Summary of Major Findings

### *Distribution of Saltuarius cornutus across Elevations and Canopy Strata.*

The northern leaf-tailed gecko is a nocturnal and arboreal rainforest obligate with a particularly cryptic habit and exceptional camouflage. Raw counts obtained in spotlighting surveys revealed a higher prevalence of leaf-tailed geckos in the lower layers of the rainforest canopy (0-5 m), and a generally higher abundance midrange along the orographic gradient. However, an analysis taking into account variations in detectability indicated that leaf tails may occupy rainforest habitats quite evenly across elevations.

Whether ones' aim is to estimate abundance, occupancy or any other form of population statistic, more recent methods require researchers to include a measure of detectability across relevant gradients (Boulinier et al. 1998; Yoccoz et al. 2001; McKensie et al 2002; Royle and Nichols 2003; O'Connell et al. 2006; Kery 2011). The generally low and variable numbers of individuals observed during spotlighting surveys led me to consider detection bias as a function of mainly canopy height and air temperature, respectively as indices of visibility and lizard activity (warmer temperatures resulting in greater activity). As a result of cryptic behaviour and efficient camouflage, detection probabilities near the ground were low and nearly absent in the emergent canopy. Adjusting for detectability allowed me to calibrate raw counts and more precisely describe distributional patterns.

Abundance is certainly a key metric to consider in studies of population dynamics, but is more difficult to estimate then occupancy (MacKensie et al. 2002; MacKensie et al. 2005). In addition to this, occupancy is closely related to abundance and is becoming the preferred measure of population state, particularly relevant in metapopulation studies (MacKensie et al. 2002; Royle and Nichols 2003; MacKensie et al. 2005). Occupancy or abundance models use the same presence-absence data to make predictions, however the most significant conclusions for conservation and management would be drawn from examining both measures (He and Gaston 2003). Examining predictions of both occupancy and abundance provided insight into leaf-tailed gecko occurrence indicating that they were probably more abundant than originally thought, because they are difficult to detect. The extent to which these geckos use the emergent canopy means that a large part of the population remains undetected, and adds strongly to the variability in detection probability. Once this detection bias is removed, both estimates stabilize across elevations and the models predict an evenly distributed population of *S. cornutus* across the orographic gradient. Leaf-tailed geckos are a strictly arboreal rainforest species, but these models predict a relatively constant occurrence across their range. The sites used in this analysis include only rainforest-type habitats, but *Saltuarius cornutus* has also often been sighted in neighbouring wet sclerophyll forests (pers. obs).

### ***Thermoregulation in a nocturnal, arboreal gecko.***

Investigating the canopy's thermal strata was an important part of describing the thermoregulatory ecology of leaf-tailed geckos. Recorded air temperatures revealed strong diurnal stratification. The emergent canopy heated more quickly and to a higher maximum temperature than canopy layers closer to the ground, which were subject to cooler temperatures and greater thermal stability. In terms of thermoregulation, this offered any arboreal ectotherm a great range of available temperatures in a relatively small physical space, allowing individuals to find new thermal microhabitats by moving just a few meters vertically. This belies the usual image of rainforest as thermally homogeneous.

The notion of diurnal thermoregulation in nocturnal, lizards such as *Saltuarius cornutus* is well documented in the literature, and my study revealed evidence that leaf-tail geckos actively seek significantly warmer diurnal retreats by occupying the emergent parts of the canopy. Similar behaviour has been observed in other geckos, in which diurnal habitat use and posture allowed individuals to rise their body temperature (Angilletta et al. 1999; Angilletta and Werner 1998; Kearney and Predavec 2000; Kearney 2001). Even if not used for locomotion, increased body temperatures during their inactive period allows geckos to maintain higher performances in other physiological processes (i.e. digestion, growth, gamete production & reproduction) than if they maintained low body temperatures all day (Autumn and DeNardo 1995; Angilletta et al. 1999; Weeks and Espinoza 2013; Kearney and Predavec 2000). Experienced temperatures of leaf-tailed geckos often surpassed recorded diurnal environmental (air) temperatures, and did so to an extent greater than that expected from hysteresis or occasional small microclimatic variations. The canopy's thermal layers converged nocturnally and having lost their thermoregulatory advantage, the geckos were observed moving and foraging more evenly throughout the canopy, although other reasons for diurnal canopy use and nocturnal movement, such as predator avoidance, could not be discounted. Nocturnal experienced temperatures slowly converged with air temperatures as recorded by surrounding data loggers.

These results showed considerable use of the emergent canopy, which was consistent with the findings from chapter 2, both suggesting a previously unobserved and unquantified use of the canopy by a nocturnal arboreal lizard in tropical rainforests. The combined information from both studies is very relevant to the conservation of these geckos, as it suggests they may not be as vulnerable to changes in climate as previously envisaged (Williams 2002). Conclusions regarding population size reveal the gecko likely occurs consistently across the region, as most variability in previous estimates of population size can be attributed the great range in detection probability across sites. In addition to this, behaviour and habitat use show a preference for warmer and more thermally variable microhabitats, which in turn leaves cooler and buffered retreats available within reach, should extremes in climate negatively affect these animals. In conclusion, leaf-tailed geckos are likely to have ways of reducing their exposure to a changing climate, therefore limiting their vulnerability. Arboreality is key to these animals' success throughout the region, offering greater thermal variability across topographical gradients and allowing the species to find a certain consistency in thermal habitat through active behavioural thermoregulation (Scheffers et al. 2013).

# Literature cited:

Aguilar, R. and F. B. Cruz (2010). "Refuge use in a Patagonian nocturnal lizard, Homonota darwini: the role of temperature." Journal of Herpetology 44(2): 236-241.

Angilletta Jr., M. J., Bennett, A. F., Guderley, H., Navas, C. A., Seebacher, F. and Wilson, R. S. (2006). "Coadaptation: A Unifying Principle in Evolutionary Thermal Biology." Physiological and Biochemical Zoology 79(2): 282-294.

Angilletta, M. J., Jr., Montgomery, L. G. and Werner, Y. L. (1999). "Temperature Preference in Geckos: Diel Variation in Juveniles and Adults." Herpetologica 55(2): 212-222.

Angilletta, M. J., Niewiarowski, P. H. and Navas, C. A. (2002). "The evolution of thermal physiology in ectotherms." Journal of Thermal Biology 27(4): 249-268.

Angilletta, M. J., Jr. and Y. L. Werner (1998). "Australian Geckos Do Not Display Diel Variation in Thermoregulatory Behavior." Copeia 1998(3): 736-742.

Aubret, F. and R. Shine (2010). "Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms?" The Journal of Experimental Biology 213(2): 242-248.

Autumn, K., Farley, C. T., Emshwiller, M. and Full, R. J. (1997). "Low Cost of Locomotion in the Banded Gecko: A Test of the Nocturnality Hypothesis." Physiological Zoology 70(6): 660-669.

Autumn, K., Jindrich, D., DeNardo, D. and Mueller, R. (1999). "Locomotor Performance at Low Temperature and the Evolution of Nocturnality in Geckos." Evolution 53(2): 580-599.

Autumn, K. and D. F. D. Nardo (1995). "Behavioral Thermoregulation Increases Growth Rate in a Nocturnal Lizard." Journal of Herpetology 29(2): 157-162.

Bailey, L. L., Simons, T. R. and Pollock, K. H. (2004). "Estimating site occupancy and species detection probability parameters for terrestrial salamanders." Ecological Applications 14(3): 692-702.

Blevins, E. and K. A. With (2011). "Landscape context matters: local habitat and landscape effects on the abundance and patch occupancy of collared lizards in managed grasslands." Landscape Ecology 26(6): 837.

Blevins, E. and With, K. A. (1998). "Estimating Species Richness: The Importance of Heterogeneity in Species Detectability." Ecology 79(3): 1018-1028.

Buckley, L. B. (2008). "Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. ." The American Naturalist 171(1): E1-E19.

Coombs, A. B., Bowman, J. and Garroway, C. J. (2010). "Thermal Properties of Tree Cavities During Winter in a Northern Hardwood Forest." The Journal of Wildlife Management 74(8): 1875-1881.

Davies-Colley, R.J., Payne, G.W. and Van Elswijk, M. (2000). "Microclimate gradients across a forest edge." New Zealand Journal of Ecology: 111-121.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. (2008). "Impacts of climate warming on terrestrial ectotherms across latitude." Proceedings of the National Academy of Sciences 105(18): 6668-6672.

Durso, A. M., Willson, J. D. and Winne, C. T. (2011). "Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes." Biological Conservation 144(5): 1508-1515.

Graham, C. H., Moritz, C. and Williams, S. E. (2006). "Habitat history improves prediction of biodiversity in rainforest fauna." Proceedings of the National Academy of Sciences of the United States of America 103(3): 632-636.

Hare, K. M., Pledger, S., Thompson, M. B, Miller, J. H. and Daugherty, C. H. (2010). "Nocturnal lizards from a cool-temperate environment have high metabolic rates at low temperatures." Journal of Comparative Physiology B 180(8): 1173-1181.

He, F. and K. J. Gaston (2003). "Occupancy, spatial variance, and the abundance of species." The American Naturalist 162(3): 366-375.

Houghton, J. T., Ding, Y.D.J.G., Griggs, D. J., Noguer, M., Van Der Linden, P. J., Dai, X., Maskell, K. and Johnson, C.A. (2001). "Climate change 2001: the scientific basis."

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. Biology of the Reptilia, Citeseer.

Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J. and Garland, T. (2009). "Why tropical forest lizards are vulnerable to climate warming." Proceedings of the Royal Society B: Biological Sciences 276(1664): 1939-1948.

Huey, R. B. and J. G. Kingsolver (1993). "Evolution of Resistance to High Temperature in Ectotherms." The American Naturalist 142: S21-S46.

Hughes, L. (2000). "Biological consequences of global warming: is the signal already apparent?" Trends in Ecology & Evolution 15(2): 56-61.

Isaac, J. L., Vanderwal, J., Johnson, C. N. and Williams, S. E. (2009). "Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates." Diversity and Distributions 15(2): 280-288.

Kearney, M. (2001). "Postural thermoregulatory behavior in the nocturnal lizards Christinus marmaratus and Nephrurus milii (Gekkonidae)." Herpetological Review 32(1): 11.

Kearney, M. and M. Predavec (2000). "Do Nocturnal Ectotherms Thermoregulate? A Study of the Temperate Gecko Christinus marmoratus." Ecology 81(11): 2984-2996.

Kearney, M., Shine, R. and Porter, W. P. (2009). "The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming." Proceedings of the National Academy of Sciences 106(10): 3835-3840.

Kéry, M. (2011). "Towards the modelling of true species distributions." Journal of Biogeography 38(4): 617-618.

Kingsolver, J. G. (2009). "The Well-Temperatured Biologist." The American Naturalist 174(6): 755-768.

MacKenzie, D. I. and W. L. Kendall (2002). "How should detection probability be incorporated into estimates of relative abundance?" Ecology 83(9): 2387-2393.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. and Franklin, A. B. (2003). "Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly." Ecology 84(8): 2200-2207.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. J. and Langtimm, C. A. (2002). "Estimating site occupancy rates when detection probabilities are less than one." Ecology 83(8): 2248-2255.

MacKenzie, Darryl I., Nichols, J. D., Sutton, N., Kawanishi, K. and Bailey, L.L. (2005). "Improving inferences in population studies of rare species that are detected imperfectly." Ecology 86(5): 1101-1113.

Mazerolle, M. J., Bailey, L. L., Kendall, W. L., Royle, A. J., Converse, S. J. and Nichols, J. D. (2007). "Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies." Journal of Herpetology 41(4): 672-689.

Meynecke, J.-O. (2004). "Effects of global climate change on geographic distributions of vertebrates in North Queensland." Ecological Modelling 174(4): 347-357.

Milly, P. C. D., Wetherald, R. T., Dunne, K. A. and Delworth, T. L. (2002). "Increasing risk of great floods in a changing climate." Nature 415(6871): 514-517.

Nicolai, V. (1986). "The bark of trees: thermal properties, microclimate and fauna." Oecologia 69(1): 148-160.

O'Connell, A. F., Talancy, N. W., Bailey, L. L., Sauer, J. R., Cook, R. and Gilbert, A. T. (2006). "Estimating Site Occupancy and Detection Probability Parameters for Meso-

And Large Mammals in a Coastal Ecosystem." Journal of Wildlife Management 70(6): 1625-1633.

Paaijmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C. and Thomas, M. B. (2013). "Temperature variation makes ectotherms more sensitive to climate change." Global Change Biology 19(8): 2373-2380.

Parmesan, C. (2006). "Ecological and Evolutionary Responses to Recent Climate Change." Annual Review of Ecology, Evolution, and Systematics 37(1): 637-669.

Parmesan, C. and G. Yohe (2003). "A globally coherent fingerprint of climate change impacts across natural systems." Nature 421(6918): 37-42.

Pinowski, J., Haman, A., Jerzak, L., Pinowska, B., Barkowska, M., Grodzki, A. and Haman, K. (2006). "The thermal properties of some nests of the Eurasian Tree Sparrow Passer montanus." Journal of Thermal Biology 31(7): 573-581.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. and Pounds, J. A. (2003). "Fingerprints of global warming on wild animals and plants." Nature 421(6918): 57-60.

Roughton, C. M. and P. J. Seddon (2006). "Estimating site occupancy and detectability of an endangered New Zealand lizard, the Otago skink (Oligosoma otagense)." Wildlife Research 33(3): 193-198.

Royle, J. A. and J. D. Nichols (2003). "Estimating abundance from repeated presence–absence data or point counts." Ecology 84(3): 777-790.

Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A. and Williams, S. E. (2013). "Increasing arboreality with altitude: a novel biogeographic dimension." Proceedings of the Royal Society of London B: Biological Sciences 280(1770).

Shaw, R. H., Hartog, G. and Neumann, H. H. (1988). "Influence of foliar density and thermal stability on profiles of Reynolds stress and turbulence intensity in a deciduous forest." Boundary-Layer Meteorology 45(4): 391-409.

Webb, J. K., Pringle, R. M. and Shine, R. (2004). "How Do Nocturnal Snakes Select Diurnal Retreat Sites?" Copeia 2004(4): 919-925.

Webb, L. and J. Tracey (1994). "The rainforests of northern Australia." Australian vegetation: 87-130.

Weeks, D. M. and R. E. Espinoza (2013). "Lizards on ice: Comparative thermal tolerances of the world's southernmost gecko." Journal of Thermal Biology 38(5): 225-232.

Williams, S. E., Bolitho, E. E. and Fox, S. (2003). "Climate change in Australian tropical rainforests: an impending environmental catastrophe." Proceedings of the Royal Society of London. Series B: Biological Sciences 270(1527): 1887-1892.

Williams, S. E. and J. Middleton (2008). "Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change." Diversity and Distributions 14(1): 69-77.

Yoccoz, N. G., Nichols, J. D. and Boulinier, T. (2001). "Monitoring of biological diversity in space and time." Trends in Ecology & Evolution 16(8): 446-453.