Evolution and Ecology of the Prehensile-Tailed Skink – *Corucia zebrata*

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TABLE OF CONTENTS

Abstract

A complete understanding of species' ecology spans a number of biological disciplines and includes the distribution and genetical lineages and how these lineages correspond with geological features in space and time, the properties of single populations (group composition, neighbourhood size and population size), habitat preferences and the behaviour and movement pattern of single individuals. This study focused on the large and ecologically atypical prehensile-tailed skink (*Corucia zebrata*), a reptile endemic to the Solomon Archipelago. Due to its large size and unusual ecology, *C. zebrata* is regarded as one of the most unique reptiles word wide, however very little information about the species exists beyond that of anecdotal nature. This thesis explores the ecology of *C. zebrata* with specific focus on phylogeography, population genetics and population size, habitat preferences and behaviour. Specifically, the aims of the thesis were to 1) Define biogeographic regions for *C. zebrata,* determine levels of divergence between island populations and assess these patterns in light of information on Pleistocene land bridges, island isolation and island age. 2) Explore the group composition and overall population structure of one *C. zebrata* population with inferences on social behaviour. 3) Explore the habitat preferences and home range size of *C. zebrata* with comparisons to other terrestrial and arboreal taxa of similar size. 4) Assess the effective and census population sizes of one *C. zebrata* population with inferences on the conservation status of the population.

For phylogeographic analysis, 61 *C. zebrata* were sampled from 14 locations across the Solomon Archipelago and sequenced at two mitochondrial loci and four nuclear loci for assessment of population differentiation and Bayesian phylogenetic inference. These data were regarded in light of geological information on Pleistocene land bridges and island age. The fine scale genetic structure of one population was assessed from a sample of 51 lizards captured in a 900 ha study plot within a larger area of continuous rainforest on Ugi Island, Makira Province. Bayesian assignment analysis and pair-wise relatedness between individual lizards based on eight polymorphic DNA microsatellite loci were used to investigate population structure and group composition. Additionally, these loci were used to estimate the effective population size on Ugi Island, and were, together with estimations on population census, used for conservation assessment. For assessment of movement patterns, a six-week study of *C. zebrata* on Ugi Island was conducted to determine home-range sizes and overlap among conspecifics. During this time, 25 lizards were fitted with radio transmitters and were followed for periods of 5–38 days.

Populations of *C. zebrata* on separate islands were found to be genetically distinct from each other, with reciprocal monophyly on mitochondrial DNA. Populations on islands connected by Pleistocene land bridges were marginally less divergent than from other nearby but isolated

islands. There are indications that *C. zebrata* has radiated across the eastern islands of the archipelago within the last 1 - 4 million years. Genetic analysis of the population on Ugi Island indicated that the connectivity within the population was high as all animals constituted a single genetic group and there were indications of a high dispersal rate across the sample area. There was ambiguous evidence for social associations of family groups. Telemetry results indicated that the average home range over the period studied was equivalent to the canopy of one tree. Assessment into population size indicated no immediate concern for the population on Ugi; however this cannot be extrapolated to populations on the remainder of the archipelago.

Data in this thesis suggest that dispersal between islands is very limited and that barriers to gene flow exist within the major islands. Phylogeography of *C. zebrata* is not explained by Pleistocene land bridges. The population genetic results indicated that there may be some short-term family association in this species, but potential social adaptations do not affect the overall genetic structure of the population. It was noted that the conventional survey methods that involve searching tree trunk habitats have low detection probability and that the detection probability is heterogeneous with respect to the habitat (tree species) and region of the country. These are important considerations for further ecological studies of the species, in particular for the purpose of assessing its conservation status.

Publications and Presentations

The thesis is based on the following articles and conference publications:

Accepted journal publication:

Hagen, I.J. & Bull, C.M. (2011) Home Ranges in the Trees: Radio Telemetry of the Prehensile Tailed Skink, *Corucia zebrata. Journal of Herpetology,* **45**, 22-25. This publication appears in Chapter 4.

Submitted journal publication:

Hagen, **I.J.,** Donnellan, S., Herfindal, I. & Bull, C.M. Hanging about in Trees: Population Genetic Structure of the Prehensile Tailed Lizard, *Corucia zebrata.* Submitted to Wildlife Research. This manuscript appears in Chapter 3.

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Conference publications:

'Conservation genetics of *Corucia zebrata* and implications for conservation planning and management'. ESF Conservation Genetics Conference, Trondheim, Norway, May 2009. Oral presentation. Data from this presentation appears in Chapter 2.

'Phylogeography of Endemic Taxa Across the Solomon Archipelago'. 6th World Congress of Herpetology, Manaus, Brazil, August 2008. Oral presentation. Data from this presentation appears in Chapter 2.

'Genetic N_e and conservation assessment of elusive species; a case study of the Solomon Islands prehensile tailed skink (*Corucia zebrata*)'. Sustainable Conservation – Bridging the Gap, Trondheim, March 2010. Poster presentation. Data from this presentation appears in Chapter 5.

'Evolution of Social Behaviour in *Egernia* Group of Australasian Skinks'. European Society for Evolutionary Biology (ESEB), Turin, August 2009. Poster presentation. Data from this presentation appears in Chapter 3.

Declaration

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for the degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference in made in the text.

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CHAPTER 1

General Introduction

A *C. zebrata* from the Western Province.

Introduction

This thesis explores the evolution and ecology of the scincid lizard *Corucia zebrata* and is divided into three parts: 1) phylogeography of *C. zebrata* across the Solomon Archipelago, 2) the genetic structure and inferred social behaviour as well as the effective size of one *C. zebrata* population, and 3) the home range usage and movement pattern of individual *C. zebrata*. This partitioning covers three major disciplines in evolution and ecology: 1) island biogeography and phylogeography, 2) population genetics and fine scale structure, and 3) field ecology. Information derived from these disciplines sheds light on different aspects of a taxon's ecology. Broad ecological knowledge facilitates successful conservation management, which in light of the current extinction crisis is more important than ever before in human history. These disciplines are reviewed in turn below. Not all the methodology described below has been applied in this thesis, but has been included in the introduction because of their importance in ecology.

Island Biogeography and Phylogeography

Biota on islands are generally the result of founder speciation or vicariance. The former implies that the species became established on an island after an immigration event, whilst the latter implies that an island has been separated from a land mass and has carried a part of a population from the larger landmass into isolation and that there has been subsequent divergence (Whittaker & Fernandez-Palacios, 2007). The separation of New Zealand from Australia is an excellent example of a vicariance event. On New Zealand, a part of the unique Gondwanan biota was carried into isolation and maintained there for approximately 80 million years with taxa becoming extinct or evolving in a different direction on the Australian continent (Ronquist, 1997). Hawaii, on the other hand, represents islands that have emerged from the sea and with biota that has established itself through migration events from the mainland or nearby islands (Rubinoff, 2008). Island systems are of significant interest to ecologists as they represent a simpler ecological system than the mainland. The geological histories of islands are often known and their boundaries are discrete. Populations on islands can therefore be easily defined (Grant, 1998). These qualities make excellent conditions for studying colonisation histories and evolution. The interest in islands as natural evolutionary experiments was first pointed out by Darwin (1859) and the concept has been developed in detail by MacArthur & Wilson (1967). Island biogeography has grown from being a discipline assessing the relationship between island size, species number and colonisation rate of different species groups, to including complex analyses of the phylogeography of island species. Phylogeography is defined as "the assessment of the correspondence between phylogeny and geography" (Avise *et al.*, 2000) and is used to describe the geographic structure of genetic lineages within and between species. Relationships between genetic lineages, levels of divergence between lineages and island geology are important parameters during assessment of historical colonisation patterns and have been significant in the development of biogeographical and evolutionary theories. The Solomon Archipelago is particularly interesting in this respect. As the islands of the archipelago have remained isolated from any continental mainland since they were formed, the biota on the Solomon Islands is a direct result of founder speciation, rather than vicariance. Moreover, some current islands within the archipelago were connected during the Pleistocene glacial cycles. Biota on islands that were connected by Pleistocene land bridges often show decreased genetic distance compared to islands that have remained isolated (e.g. Heaney *et al.* (2005); Pulvers & Colgan (2007)). Historical colonisation patterns of a number of taxa on the Solomon Archipelago are now being explored with molecular genetic methods (e.g. Filardi & Smith (2005); Pulvers & Colgan (2007)) and are important in order to understand the origins of the Pacific biota. There is currently no detailed study of the phylogeography of Solomon Archipelago reptiles, as previous studies have focused on birds and bats, which have much wider dispersal abilities than reptiles. Phylogeography of a reptile will therefore add information based on a taxon with a lower dispersal ability than avian species. Such broad knowledge of historical colonisation patterns is important not only for expanding our understanding of the geological events that shape the biogeography of biota, but also to maximise the outcomes of conservation management by incorporating more species.

Models of evolution

Different parts of the genome evolve at different rates. Intronic or non-coding sections of the nuclear genome evolve at a faster rate than do protein coding regions (Lemey *et al.*, 2009). Similarly, highly conserved regions coding for proteins that are vital for survival evolve slower than coding regions that tolerate mutations without major fitness outcomes. The mitochondrial (and chloroplast) genome has the benefit (for researchers) of a high rate of evolution (George *et al.*, 1979) as well as maternal inheritance, with subsequent low effective population size and a low or negligible rate of recombination (Harrison, 1989; Meiklejohn *et al.*, 2007). As such it has proven an extremely useful tool for phylogenetic inference and to identify species or population boundaries (Avise *et al.*, 1987; Arèvalo *et al.*, 1994; Austin *et al.*, 2010). Within protein coding sections of the nuclear and the mitochondrial genomes, the nucleotides on the 1st, 2nd and 3rd position do not evolve at the same rate. This is due to changes in the 3rd codon position being less likely to change the protein structure than changes in the 2nd or 1st codon position (Lemey *et al.*, 2009). The nucleotide bases themselves; pyrimidines (C and T) and purines (A and G), have different properties. Transitions (changes within purines or pyrimidines) and tranversions (changes from purine to pyrimidine or opposite) may not occur at the same rate (Lemey *et al.*, 2009). When inferences on the phylogeny are made, one must therefore apply the correct model of nucleotide substitution not only to the different loci under investigation, but also to the different nucleotide positions. A number of nucleotide substitution models have been developed, and only the most applicable to my study are mentioned below. The simplest model is the JC (Jukes and Cantor) model (Jukes & Cantor, 1969), which assumes that all substitutions occur at the same rate and that the four nucleotides occur at equal frequencies. The K80 model takes the different rates of transitions and transversions into consideration, whilst assuming equal base frequencies (Kimura, 1980). The HKY model on the other hand, distinguishes between transitions and transversions whilst allowing for different frequencies of the different bases (Hasegawa *et al.*, 1985). Lastly, the GTR (Generalised Time Reversible) allows each individual substitution to have a different rate and be time reversible and for different frequencies of the each of the bases (Tavare, 1986; Waddell & Steel, 1997). The appropriate model must be selected and implemented prior to phylogenetic inference as the choice of model may significantly influence the inference of tree topology and branch length (Ward *et al.*, 2010). This is done by comparing the likelihood of a tree estimated with each of the different models given the DNA sequence data and then ranking the different models according to AIC scores (Akaike, 1979).

Phylogenetic inference

A number of approaches with fundamental theoretical differences have been developed for the estimation of phylogenetic trees from nucleotide sequence data. The most important distinctions are analyses based on distance methods, maximum parsimony, maximum likelihood methods and Bayesian inference (Lemey *et al.*, 2009).

Distance methods (neighbour-joining and UPGMA) are based on comparing the genetic distance between pairs of sequences and storing the distance information in a distance matrix. Such pair-wise comparisons are done for all sequences in an alignment and the information in the matrix is then used to build a phylogenetic tree where the closest branches have the least genetic difference in the matrix (Felsenstein, 1988). The method is quick and produces a tree with a good indication of the evolutionary distance between the different taxa represented in the tree. However, the distance method is a non-character based approach where the phylogenetic information is compressed into a single value for each pair. The method is therefore not able to capitalise on the large amount of information that is found within the characters of the alignment, although some information can be retained by selecting the appropriate model of evolution (Lemey *et al.*, 2009). The distance method has been largely replaced by maximum likelihood or Bayesian inference (reviewed below) but is still regarded as an excellent method to generate a 'first pass' at data sets and to identify reliability issues with the data. Trees generated from distance methods are also used to compare nucleotide substitution models (Nylander, 2004).

The maximum parsimony (MP) method is a character based approach that defines the best tree typology as the one that requires the least amount of character changes to explain the observed states (Lemey *et al.*, 2009). The maximum likelihood (ML) method is also character based and uses the information in the sequence alignment to maximise the likelihood of observing a given sequence based on the tree topology, branch lengths, model of nucleotide substitution, (Lemey *et al.*, 2009). The ML approach is used frequently (e.g. Kasapidis *et al.* (2005); Parent & Crespi (2006); Kirchman & Franklin (2007); Smith & Filardi (2007); Giannini *et al.* (2008); Ursenbacher *et al.* (2008)) and is beneficial in that it allows for the opportunity to investigate the statistical support for a range of different evolutionary scenarios (Lemey *et al.*, 2009). However, an exhaustive search for all possible scenarios can be done only for a taxon set of 10 or less. Beyond this, only a subset of the possible evolutionary scenarios can be examined due to the exponential growth in the amount of potential trees with increasing number of taxa to be examined (Huelsenbeck *et al.*, 2001), but recent efficient search methodologies produce reliable estimates even for large datasets (numbers of taxa and sites), e.g. RaxML (Stamatakis *et al.*, 2008). Another advantage of the likelihood based methods (ML and Bayesian) is that the data can be partitioned allowing different models of nucleotide substitution to be applied to each partition.

Bayesian inference is character based approach that shares many of the ML method's strengths but with a more flexible method of exploring the probability distribution of possible trees given a hypothesis for the data (Huelsenbeck *et al.*, 2001). Bayesian analysis (see Huelsenbeck *et al.* (2001) for review) has become one of the frequently used methods for phylogenetic inference. The prior is defined by the user by specifying the models of nucleotide substitution for the different loci in the analysis. The posterior probabilities of the analysis are obtained by exploring the 'tree-space' using the Markov chain Monte Carlo (MCMC) sampling technique. The sampled trees are summarised into a consensus tree, where the posterior probabilities are presented for all branches. Although statistically robust and frequently used to infer phylogeny, Bayesian inference (and ML) depends on an appropriate model to describe the process that produced the data. Specifying inappropriate models may lead to misled posterior support in the results, but many datasets are robust to minor violations of the model. Additionally, the Bayesian approach is sensitive to over-parameterising of the data. As the number of parameters in the model increase (such as a high number of data partitions), the data to be analysed must have significantly more information than when simple models are applied (Lemey *et al.*, 2009).

Phylogenetic models can be used to date splits in the tree that conform to particular events of interest (i.e. colonisation or speciation events). For this to be possible the evolutionary rate of the loci used for inference must be determined using calibration points. These calibration points are generally based on fossil calibration with the subsequent problem that a detailed fossil record is lacking for many species (Sanders & Lee, 2007), or known dates for island emergence when dating island colonisation or splits between endemic island species (Benavides *et al.*, 2009). The reliability of the analysis is therefore limited by the availability of calibration points, and the amount of information to inform reconstruction methods (e.g. a large distance to outgroup or external calibrations with no intervening taxa to sample), and substitutional saturation (e.g., if fast evolving genes are used with deeply divergent external calibrations). A number of speciation and colonisation events have been reliably dated, such as the colonisation of the Galapagos Islands by lava lizards (Benavides *et al.*, 2009), the divergence times of three filesnakes using fossil calibrations (Sanders *et al.*, 2010) and the radiation of several lineages of Australian geckos (Oliver & Sanders, 2009).

When conducting the analysis described above it is desirable to include an outgroup amongst the taxa to be examined. The outgroup provides information on the direction at which evolution has occurred, and whether a particular state is derived or original. An outgroup should ideally be closely related to the ingroup so that it can be unambiguously aligned with the in-group taxa, yet belong to distinct lineage (Lemey *et al.*, 2009). Using an inappropriate outgroup may lead to erroneous phylogenetic inference, in particular problems with assigning the root node for the ingroup (Piller & Bart, 2009).

Population genetics

The assessment of population characteristics using standard field techniques (reviewed below) can be logistically difficult and may involve several seasons of field work. Traditional field techniques may not be practical for elusive species inhabiting inaccessible habitats. However, many ecological parameters may be estimated from molecular genetic analysis of a subset of the population using a single season of sample collection and are therefore an alternative that offers greater logistical ease. In particular, molecular genetic methods may yield detailed data on the fine scale population structure, dispersal patterns and the social structure of a population. For example, a higher relatedness in one sex compared to the other sex in a geographically clustered sample indicates that dispersal is biased towards the sex with the lowest relatedness (Gardner *et al.*, 2001). Parentage can be estimated and thus yield information on mating systems (Hedmark *et al.*, 2007; Olsson *et al.*, 2007), comparative reproductive success of different individuals (Gopurenko *et al.*, 2007; Serbezov *et al.*, 2010) and the degree of extra pair copulations in socially monogamous species (Stewart *et al.*, 2010). Also parameters such as neighbourhood size and overall dispersal distance can be accurately estimated with molecular genetic methods (Smith *et al.*, 2009). In this way, populations can be defined accurately and the level of migration between populations can be estimated (e.g. Peakall et al. (2003); Evanno et al. (2005); Wang (2009a)). Molecular genetic markers can also be used to calculate the number of individuals in a population, either as a direct census where the number of different genotypes are defined, or as a measure of the effective population size based on samples from a subset of the population (Luikart *et al.*, 2010). The concept of the effective population size is discussed further in Chapter 5.

Microsatellites have become the most frequently used molecular genetic marker for population studies. Microsatellites are co-dominant and hyper variable regions in the nuclear genome that provide a unique ‘genetic fingerprint’ for each individual in a population (with the exception of monozygotic twins), provided enough variable loci are available (Ellegren, 2000; Allendorf & Luikart, 2007). A microsatellite locus not subject to selection provides a neutral genetic marker. Each locus should ideally follow Mendelian inheritance, thereby allowing for easy calculation of the proportion of shared alleles between individuals. As molecular techniques improve and become more affordable Single Nuclear Polymorphism (SNP) markers have become an alternative to microsatellite markers. Like microsatellites, SNPs can be used to estimate genetic variation, identify individuals and define population boundaries and size (Morin *et al.*, 2004). Additionally, SNPs are useful for large scale QTL mapping and whole genome association studies. Few such studies have been carried out on wildlife populations, however, SNP chips with up to 10,000 SNPs are now being developed for screening in natural populations of some passerine species (Van Bers *et al.*, 2010). Much larger numbers of SNPs are required to achieve the resolving power of just a small number of highly polymorphic microsatellite loci, i.e. typically five times as many SNP loci are required. The SNP method has not been applied in this thesis.

Field ecology

Molecular genetic methods cannot replace completely traditional field techniques. Information on individual behaviour and population vital rates (birth and survival rates, reproductive rates etc.) can sometimes be more reliably acquired through traditional field work and are important for assessing the conservation status for the population. I will review some of the most common methods for population monitoring in the field; 1) radio telemetry, 2) capture – mark – recapture, and 3) habitat occupance. Radio telemetry provides information on individual behaviour whilst the two latter may yield information on population vital rates and population density.

Radio telemetry

Radio telemetry is a useful technique for assessing home range size, habitat preferences and movement patterns of animals. Several different methods have been developed for analysis of spatial data (both radio telemetry and GPS data). The most common method is to use the minimum convex polygon, which has been used in several studies of terrestrial lizards (Bull & Freake, 1999; Kerr & Bull, 2006) and mammals (Harris *et al.*, 1990). An alternative method is to determine whether an animal displays site fidelity or moves randomly. This can be done by graphing the distance the animal has moved against time and fitting the distribution against four models: linear (indicating no home range); flat (indicating a stable home range); power curve (indicating a less stable home range) and a saturation curve (indicating a stable home range) (Van Moorter *et al.*, 2009). The model fit can be ranked according to AIC scores (Akaike, 1979). This method has been used on a range of different taxa, from reptiles (Brian *et al.*, 2007) to marine species (Austin *et al.*, 2004) and large ungulates (Fryxell *et al.*, 2008; Van Moorter *et al.*, 2009). Both of the above methods are easily implemented on terrestrial animals that operate in a two dimensional habitat. Radio telemetry of arboreal animals on the other hand, is associated with a range of challenges; these are described further in Chapter 4. No clear protocol is available for home range calculations in a three-dimensional habitat, though the two-dimensional area covered by the home range is a parameter that has been used (Perry & Garland, 2000). Radio telemetry is particularly useful in generating data on habitat preferences and detection probability, both of which are vital for design of capture-mark-recapture and occupance studies.

Capture-Mark-Recapture

Provided the assumptions are met, capture-mark-recapture (CMR) provides a robust method for estimating abundance, survival, recruitment and population growth rate. It is therefore a vital tool for ecologists as many ecological parameters cannot be estimated without information derived from CMR. Notably, capture may not imply actual handling of the animal, as photo capture or identification by hair or fecal samples may provide excellent alternatives, particularly for threatened or dangerous species (Smith *et al.*, 1999; Broquet *et al.*, 2007). The study can be designed as open or closed population, however the closed population design, where no births, deaths or migration is assumed, allows for the most robust and reliable analysis (Pollock, 1982; Pollock *et al.*, 1990). A CMR study comprises T primary sampling periods across N sites, when the population is assumed to be either open or closed. Within each primary sampling period, the target species is detected in k_t secondary sampling periods of each site, allowing for estimations of species abundance and density within the study population. Primary sampling periods can be repeated, i.e. between seasons, and with a long enough interval for populations to be assumed open, thus allowing for estimations of migration and population growth rate, λ (Mills, 2007). The programme MARK (White & Burnham, 1999) is commonly used for the analyses of CMR data. Abiotic factors such as topography, geography, substrate, climate, weather conditions and time should be recorded during each sampling occasion, treated as co-variates and incorporated in the analysis as detection probabilities may be affected. Ideally, heterogeneity should be minimised by rotating the personnel and the order at which the sites are surveyed. The CMR approach yields reliable data on population parameters when stringent attention is paid to the assumptions and is widely used in population ecology (e.g. Smith *et al.* (1999); Clucas *et al.* (2008); Harris *et al.* (2010)). For species with a long generation time however, up to a decade of field work may be required before satisfactory results are reached (Clucas *et al.*, 2008).

Occupance

Proposed by Mackenzie *et al.* (2002), the occupance approach has the benefit of being inexpensive, easily exercised and allowing for staff to be easily trained, whilst providing a robust estimate of species distribution. The method is therefore an excellent option in challenging economic environments, such as in developing countries. Occupance relies on bimodal information on detection or non-detection of a species and the probability of detecting the species if it is present, in order to estimate probability of site occupancy, thereby monitoring the proportion of sites that are occupied, rather than the number of individuals present in the population. This approach is ideal for large-scale monitoring programs focused on species that are difficult to count and where the detection probability is < 1. Changes in occupancy rate can be modelled as a function of site extinction and colonisation and is as such one of the few monitoring or survey techniques capable of providing information on long term meta-population dynamics. Sample design is similar to Pollock's robust design for mark-recapture studies (Pollock, 1982; Pollock *et al.*, 1990). The detection history for each site is expressed as 1s and 0s, indicating detection and non-detection of the species. Estimates of detection probabilities (p) and the probability that a species is present (ψ) is obtained using the computer program PRESENCE (Mackenzie & Royle, 2005). The optimal number of secondary sampling occasions and number of sites must therefore be determined after detection probability and probability of species presence has been estimated. This can be achieved by repeated surveys of transects that incorporate the quantified home ranges of individuals. Detection probability may vary according to habitat type and must therefore be estimated separately for each habitat type. When detection probability and occupancy rate are estimated, the optimal balance of survey occasions (k_t) and sites (N) can be deduced from the following equation (Mackenzie & Royle, 2005):

$$k_t \times N = \frac{\psi k_t}{\mathrm{var}(\psi)}\left[(1-\psi) + \frac{(1-p^*)}{p^* - k_t p(1-p)^{kt-1}}\right] \tag{1.1}$$

where $p^* = 1 - (1 - p)^{kt}$, by solving for k_t and N, respectively. If logistically possible, an occupancy study can be combined with a traditional CMR study. The occupancy approach has been used for the New Zealand lizard *Oligosoma otagense*, for which the method is particularly appropriate since presence or absence can easily be determined by visual location of the lizards when they bask on rock outcrops and the detection probability can be estimated accurately (Roughton & Seddon, 2006).

Conservation and management

Biota on islands are subject to higher extinction rates compared to mainland species as a result of smaller population sizes, lower genetic variation and because they are disconnected from meta-populations that will normally re-seed areas of local extinction (Frankham, 1998). Biologically, any fragment of habitat that is disconnected from the meta-population and reproductively isolated can be considered equivalent to an island. Mountain tops are a classical example, as these become biological islands for alpine species that are unable to disperse across lowland habitat. Anthropologically driven habitat destruction and degradation currently turn large meta-population habitat into smaller fragmented habitat patches that effectively become biological islands. Fragmentation is currently one of the principal drivers of biodiversity loss (Gascon *et al.*, 2000). This process is driven partly by direct habitat destruction and subsequent removal of biota and indirectly through increased genetic drift and reduced gene flow within isolated sub-populations. Reduced gene flow can increase genetic variation between sub-populations, and though these effects sometimes lead to increased genetic diversity across a meta-population, sub-populations are at greater risk of extinction due to stochastic events and inbreeding depression (Lande & Barrowclough, 1987; Frankham, 2005). The severity of these effects depends not only on the extent of habitat fragmentation, degradation and destruction, but also on the initial genetic load (i.e. deleterious alleles), ecology and life history (e.g. reproductive rates or dispersal ability). Species with a high dispersal ability are often less susceptible to fragmentation, however the effects of fragmentation and disrupted genetic connectivity can even be seen in the genetic profile of highly mobile species such as coyotes and bobcats (Riley *et al.*, 2006). The effective population size is an important parameter in this respect as the number of individuals that will contribute to the next generation is almost always smaller than the total number of individuals in the population (Charlesworth, 2009). In order to assess the conservation status of a population, it is therefore necessary to study the genetic diversity, life history, mating system, habitat requirements, population numbers and population vital rates of the species.

Corucia zebrata – life history and ecology as known prior to the current study

The prehensile-tailed lizard *Corucia zebrata* (Gray, 1855) is also known as the monkey-tailed skink and the Solomon Islands tree skink. The species is one of the largest members of the family Scincidae and can reach a total length of up to 800mm (McCoy, 2006). It has evolved a number of ecological traits that are remarkable amongst skinks, such as a strictly arboreal life and obligate herbivory, however its best known feature is the prehensile tail. Being endemic to the Solomon Archipelago, it is regarded as the Solomon Islands flagship faunal species and has become a symbol of the remarkable biodiversity and endemism of its native range. Due to its large size, *C. zebrata* is important as a traditional food source for indigenous people on the Solomon Islands (pers. obs.). Despite the species' iconic status, very little has been known about its life history, basic ecology and behaviour in the wild and the available information has been based on anecdotal field observations. More specifically, the species inhabits large lowland rainforest canopies and strangler figs (*Ficus*) are reputedly a preferred habitat. As for diet, *C. zebrata* has been reported to have a preference for leaves and flowers of the climbing epiphyte *Epipremnum* (McCoy, 2006). The reproductive rate is unknown; however females give birth to a single large young (sometimes two), after a six to seven month pregnancy (McCoy, 2006). Age to sexual maturity is unknown. Life-history data, population vital rates and detection probability for the species are unquantified. The distribution of *C. zebrata* covers all major islands of the Solomon Archipelago, from Buka and Bougainville in the west, which politically belong to Papua New Guinea and to the island of Makira in the east of the Solomon Islands (Fig. 1).

Though a monotypic genus, two sub-species of *C. zebrata* have been described; *C. z. alfredschmidti* (Kőhler, 1997), the northern prehensile tailed skink and *C. z. zebrata* (Gray, 1855), the common prehensile tailed skink. The northern sub-species is described as smaller, with a snout-vent length of 70-80 mm shorter than *C. z. zebrata*, and subsequent decrease in weight. Additionally, *C. z. alfredschmidti* is reported to be brighter green with a more pronounced banding pattern. The sclera of *C. z. alfredschmidti* is black, whilst that of *C. z. zebrata* is white. Importantly, these sub-species descriptions are based on limited geographic sampling (Choiseul and the Shortland Islands were not sampled), and rely only on morphological measurements (Kőhler, 1997). McCoy (2006) suggests that animals on the Shortland Islands conform to the description of *C. z. alfredschmidti.* No molecular genetic study of the systematics of *C. zebrata* has been undertaken and this will be necessary in order to adequately test the existing sub-species hypothesis.

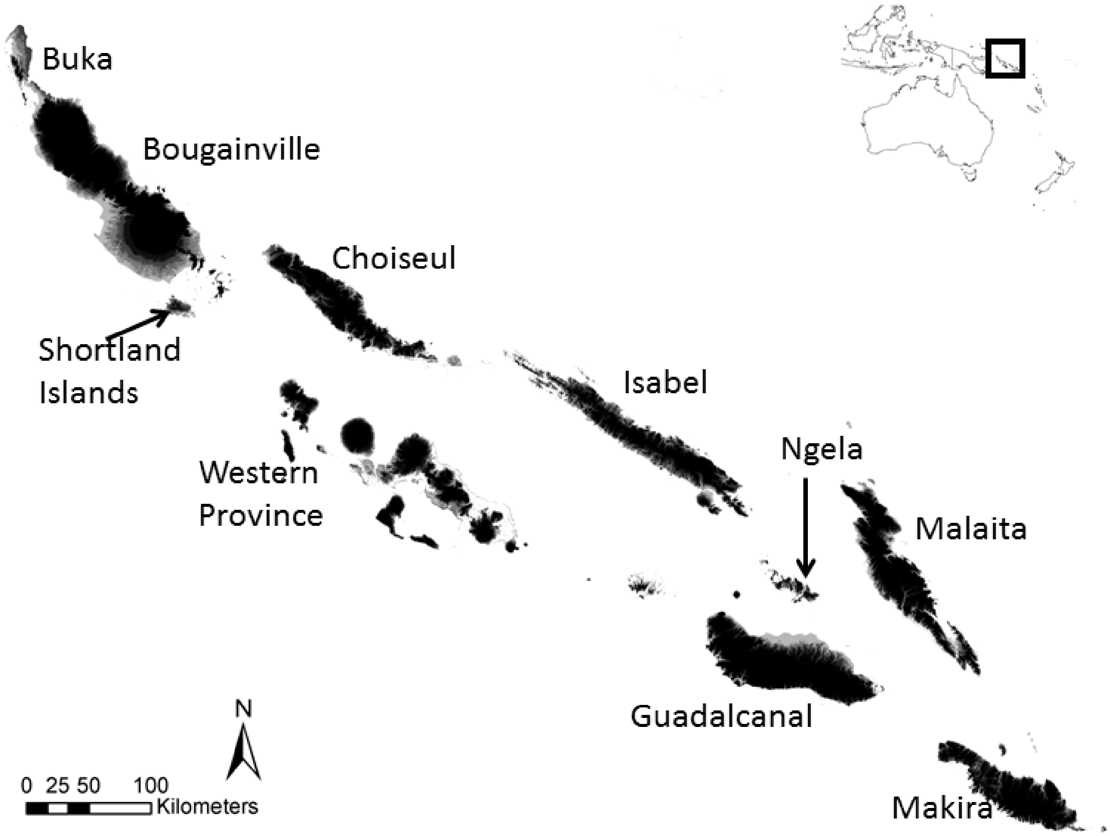

Figure 1: Map of the Solomon Archipelago.

Corucia in the wider context: the Egernia group and social behaviour

Though the prehensile tailed skink is endemic to the Solomon Archipelago, its closest relatives belong to a largely Australian group of skinks, the *Egernia* group; a distinctive lineage of skinks that currently includes 47 species in seven genera: *Bellatorias, Corucia, Cyclodomorphus, Egernia, Lissolepsis, Liopholis and Tiliqua,* (Gardner *et al.*, 2008a). Dating with molecular genetic methods shows that *Corucia* diverged from the rest of the group during the Oligocene (Skinner *et al.*, 2011) which is also the time of emergence for the Solomon Archipelago (Hall, 2002).

Most reptiles do not display any social behaviour beyond territoriality and dominance hierarchies. However the *Egernia* group is unusual in that several species have evolved highly complex social behaviours that resemble social adaptations found in birds and mammals, such as long term mating partnerships, tolerance for genetically related individuals and large, stable aggregations of related individuals. Social traits have been found in *Bellatorias*, *Egernia* and *Liopholis*, however only a few species have been studied thoroughly, and these are also the ones with the most pronounced social adaptations. Highly social species include *E. cunninghami*, *E. saxatilis* and *E. stokesii,* but the aforementioned genera also contain solitary species (such as *L. inornata* and *E. striolata* (see Chapple (2003) for a review). Species of *Egernia* (Gardner *et al.*, 2002) and *Tiliqua* (Bull *et al.*, 1998) also show a high degree of monogamous pairing, both within and between seasons and these partnerships can last over 25 years. This is another unusual trait in lizards, where, in other taxa, polygamy is the most common mating strategy. In regard to *Corucia*, there is a popular conception that the species is social to some degree, as individuals have been observed emerging from shared refugia (McCoy, 2006), however the occurrence and nature of potential aggregations have not been studied. So far behavioural ecology studies in the *Egernia* group have focused on a few species of *Egernia* and *Tiliqua*. Given the evolutionary relationship between *Corucia* and other taxa in the *Egernia* group, a study of behavioural ecology in *C. zebrata* will provide a broader perspective of the taxonomic spread of social behavior within the *Egernia* group and may further our understanding of the origin of sociality within this lineage of skinks.

Properties of the native range: geology and ecotype of the Solomon Archipelago

The Solomon Islands comprise two parallel chains of over 900 islands, extending 1,600 kilometres between Papua New Guinea and Vanuatu (Petterson *et al.*, 1999), as illustrated in Fig. 1. The larger islands have rainforest covered mountain ranges intersected by narrow valleys with coastal belts fringed by coral reefs, whilst most of the smaller islands are raised coral or low atolls. The island group is situated in the tropics and receives an annual rainfall of 3000 – 5000 mm at sea level (Mayr & Diamond, 2001). The annual weather pattern differs between the different islands of the archipelago, wherein the western islands receive the most rain during June and July, and the eastern islands facing wetter months over November – January, though no clear pattern is obvious (Mayr & Diamond, 2001). Though the topography is mountainous, the main mountain ranges are generally no higher than 1000 – 1500 metres altitude. The habitat is homogeneous across the archipelago, with the most significant habitat diversity displayed through differences in topography (e.g. lowland vs. montane rainforest). The ecotype resembles the rainforests on continental Southeast Asia and species diversity is moderately impoverished compared to expectations (Mueller-Dombois, 1998). The islands of the Solomon Archipelago emerged from the ocean 30-40 million years ago as the Indian Plate collided with the Pacific Plate (Hall, 2002). The New Georgia Group (Western Province) is the youngest part of the archipelago and is a result of volcanic activity during the Pliocene and Pleistocene and therefore no more than five million years old (Petterson *et al.*, 1999). Makira is the oldest island in the group and is geologically significantly different from the neighbouring islands of Malaita and Guadalcanal. Makira is likely to be geologically substantially older than the rest of the archipelago and Petterson *et al.* (1999) further states that Makira is “a deeply eroded piece of crust” although no dates of emergence are implied.

Several islands of the archipelago were connected during the Pleistocene glacial cycles; the last of which is believed to have reached a maximum 18,000 years ago; with sea level 120 metres lower than today (Fairbanks, 1989). Bougainville, Choiseul, Isabel and Ngela were joined and Guadalcanal would have been either connected to the same landmass or separated by a narrow channel. The Western Province was divided into two major islands. Makira and Malaita are thought to have been isolated throughout the glacial cycles (Mayr & Diamond, 2001). Details on the geology are described in more detail in Chapter 2.

Working in the region

When the work pertaining to this thesis was started there was no organisational or political infrastructure within the Solomon Islands that facilitated the development of the research presented in this text. There was no clear procedure for the application of research permits, nor was there a clear strategy for the study of an elusive arboreal lizard, and importantly, no guidelines relating to negotiations within the cultural environment in the country. A research permit was obtained after three months with the help of a scientist familiar with the circumstances - Dr Chris Filardi.

Location and capture of the study animal was a significant challenge throughout the study. The habitat of *Corucia zebrata* is largely inaccessible to field workers and a capture always involved ascending trees and searching within holes and crevices, and always with the help of local people. There were large differences in the ease with which the species was located in the separate parts of the country. The location of each animal took one week or more with the help of 4-6 people searching on Guadalcanal, whereas two days search with two people resulting in 10 lizards on Ugi Island (Makira Province). Due to the large cultural differences among local inhabitants in their willingness and ability to climb trees and capture *C. zebrata* across the archipelago it is difficult to determine if the varying success rate was due to different population densities of *C. zebrata*, different abilities (or willingness) of the people involved or a combination of the two factors.

Solomon Islands is a developing country with poorly developed infrastructure and where locations nominally connected with scheduled flights may be difficult to reach due to a high cost and unreliable connections. The cost of petrol is very high and boat travel, in small outboard powered out-rigger canoes, is therefore costly and sometimes dangerous due to treacherous conditions in open water. Most remote villages lack commercial accommodation for visitors and researchers must therefore live with local people on their premises. Although the generosity of local people is overwhelming, this arrangement has certain disadvantages as the visiting researcher must exercise extra caution in regard to local customs, with subsequent personal restrictions. Importantly, no work may be carried out unless it has been approved by the local chief. Acquiring a local 'research permit' is a time consuming process that may cause friction in the local community.

Nearly all land in the Solomon Islands is private and a researcher may therefore not attempt to walk into the forest without the approval of the local owners and a representative of the local tribe present. The accompanying person fills the role as guide and field assistant and allows the researcher to freely carry out the necessary work within the area that falls under the local tribe. As most Solomon Islanders are very hesitant to spend time outdoors at night, a researcher may find it difficult to carry out work after sunset. Although a visiting researcher means short term employment for a small number of people in the local tribe, the visitor also disrupts the daily life in the local community. Most communities are therefore reluctant to have researchers visiting for long periods, which places restrictions on long term field work. Additionally, the lack of electrical power and permanent structure accommodation means that long term visits become logistically difficult as electronic equipment will not be operating beyond battery life and may become damaged from being stored in a tropical climate without use. Indeed the attrition rate on all equipment and clothing in a hot, humid tropical environment is very high.

As of January 2008, the Solomon Islands' Government discontinued the approval of research permits to visiting researchers. The research permit for the current work was issued in July 2007 and expired in May 2008 at which point field work was terminated. All attempts to approach the appropriate authorities with application for a renewal have since been unsuccessful.

Ugi Island

The data pertaining to Chapter 3, 4 and 5 were collected from the island of Ugi in the Makira province. Ugi Island has the benefit of being relatively easy to reach, as the Makira airport is among the most reliable in the country and Ugi Island lies within an affordable 25 km boat ride from the airport and the provincial capital of Kira Kira (see Fig. 2).

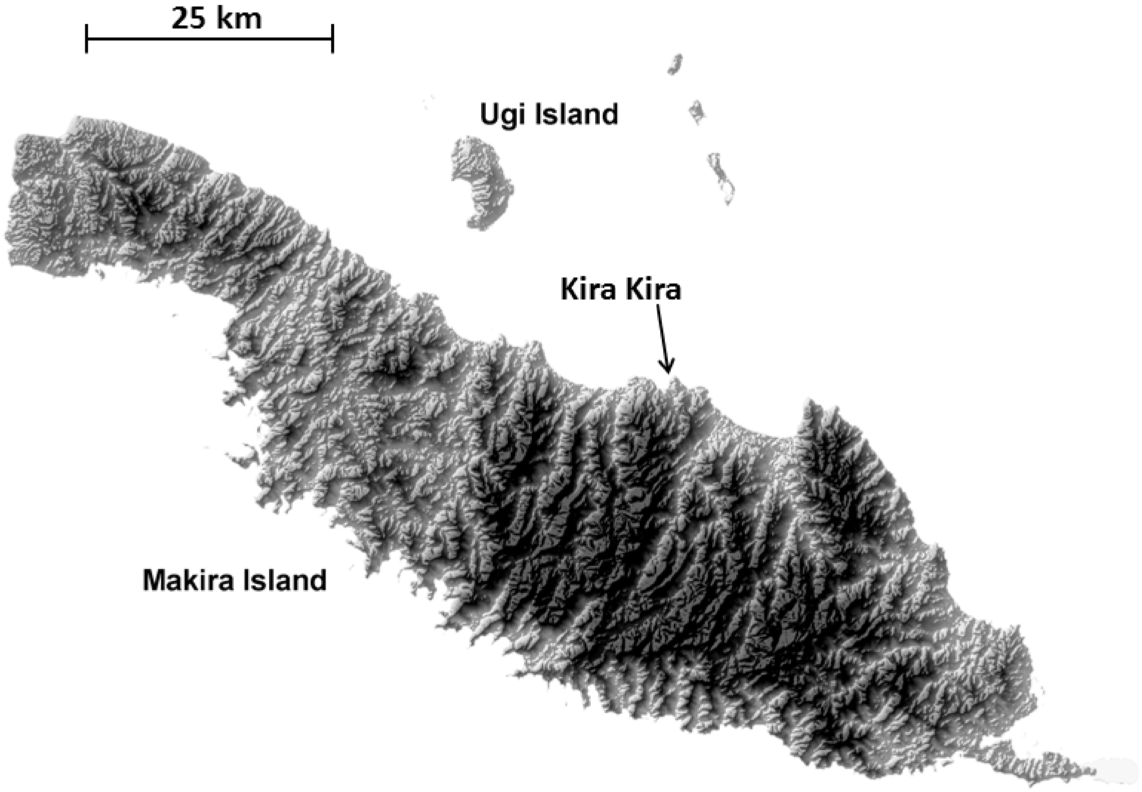

Figure 2: Ugi Island in relation to Makira. Darker areas represent higher altitudes. Ugi Island lacks major topographical features and is situated 8 km from Makira.

The total land area of the island is approximately 50 km^2 and it is scarcely populated with a number of small villages largely consisting of family groups in addition to the larger village of

Suena, which has a population of approximately 300 people. Ugi Island has not been subject to commercial clear fell logging, but there has been selective subsistence level logging and patchy clearing of forest for local agriculture. A number of mature trees have been removed from accessible parts of the island for village construction; however, the canopy has for the most part remained closed and supports a sparse understory. Virgin forest is only found on the very centre of the island. The island lacks major geographical features such as large rivers and mountains. The study area referred to in this thesis represented about 20% of the available forested *C. zebrata* habitat on the island and supported a relatively high density of *C. zebrata*. Research was made possible on Ugi Island due to extremely helpful and generous land owners as well as reliable field workers that were very experienced in finding *C. zebrata*. As such, the island is probably one of the few places in the country where the work described in Chapters 3, 4 and 5 could have been carried out.

Conservation status of C. zebrata

The conservation status of *C. zebrata* is unknown, however the species' habitat is under threat; only 0.28% of terrestrial ecosystems on the Solomon Islands are formally protected and logging operations and agriculture continue to cause habitat loss, fragmentation and degradation. The country's ecosystems therefore rank among the 10 most threatened forest regions on the planet (Wein & Chatterton, 2005). The effects of fragmentation, ongoing harvest for human consumption and export to the international pet market (McCoy, 2006; pers. obs) are unquantified. An assessment of the conservation status of *C. zebrata* is therefore due; however more information about the ecology of the species is required before such assessments can be made.

Project aims and thesis structure

This thesis is organized into four result chapters, which reflect the partitioning described above. Each of these is written in publication format with separate aims, introduction, methods, results and discussion, but with all references gathered in a complete list at the end of the thesis. This work starts with an investigation of the evolution and divergence of *C. zebrata* across the archipelago, then moves on to discuss the species on a population level, with particular attention to small scale genetic structure and inferred behaviour. I then investigated movement and behaviour of individuals of *C. zebrata*, with a discussion of how this information compares with similar data from other species of the *Egernia* group. Lastly, I assessed the census size and effective size of one *C. zebrata* population, by the use of information presented in earlier chapters. This way, I endeavor to fill some of the gaps of knowledge about the biology of *C. zebrata* and aid in the development of an assessment of the conservation status and management recommendations for the species.

Chapter 4 has been accepted as a publication in Journal of Herpetology. Chapter 2 is about to be submitted to Journal of Biogeography whilst Chapter 3 has been submitted to Wildlife Research and is in review as of Jan 21 2011. Chapter 5 may be adapted for a publication at a later date. With the exception of the references, which are in a single format throughout the thesis, Chapters 2, 3 and 4 are presented in the form at which they have been (or will be) submitted to the respective journals or accepted for publication. The four results chapters address the aims of the study as listed below.

Aim 1 Investigate the phylogeography and colonisation pattern of *C. zebrata* across the archipelago, and use information on genetic lineages to define ESUs and MUs for the species (Chapter 2).

Aim 2 Investigate fine scale population structure and dispersal pattern within islands for *C. zebrata* (Chapter 3).

Aim 3 Investigate habitat preferences and home range size for individuals of *C. zebrata* (Chapter 4).

Aim 4 Make inferences on the census size (N_c) and effective population size (N_e) of a population of *C. zebrata* (Chapter 5).

CHAPTER 2

Phylogeography and Colonization Pattern of *Corucia zebrata* on the Solomon Archipelago

To be submitted to Journal of Biogeography

A *C. zebrata* from the Shortland Islands.

Abstract

Aim Define biogeographic regions for *Corucia* (Gray, 1855) and determine level of divergence between island populations in light of Pleistocene land bridges, island isolation and island age.

Location The genus is endemic to the the Solomon Archipelago in Northern Melanesia.

Methods *Corucia zebrata* was sampled from 14 locations across the Solomon archipelago and sequenced at two mitochondrial loci (*ND2* and *ND4*; 1697 bp in total) and four nuclear loci (*AKAP9*, *β-fibrinogen*, *PTPN12* and *rhodopsin*; 2834 bp in total). Measures of genetic distance, analyses of genetic variation and Bayesian phylogenetic inference were used. These data were assessed in light of geological information on Pleistocene land bridges and island age.

Results Populations of *C. zebrata* on separate islands were found to be genetically different from each other, with reciprocal monophyly on mitochondrial DNA. Populations on islands previously connected by Pleistocene land bridges were marginally less divergent from each other than from populations on other nearby but isolated islands. There are indications that *C. zebrata* has radiated across the eastern islands of the archipelago within the last 1 - 4 million years.

Main Conclusion Analyses of the data suggest that genetic distances calculated for mitochondrial genotypes are partly explained by isolation by distance; that dispersal between islands has been very limited and that there are barriers to gene flow within the major islands. Islands that have been isolated during the Pleistocene glacial cycles are somewhat divergent in their mitochondrial genotypes, however, isolation by distance and recent colonisation of isolated but geologically younger islands appear to have had stronger effects on the phylogeography of *C. zebrata* than the Pleistocene glacial cycles. This contrasts with patterns reported for avain taxa, and highlights that biogeographic regions for island species cannot be directly extrapolated among taxa of differing dispersal ability.

Introduction

Islands represent natural laboratories that allow for simpler examination of evolution and ecology than is possible on large continental landmasses. They have been the focus of a number of seminal studies. Amongst those Darwin's exploration of the Galapagos remains the most revered and fascinating. Long periods of geographic isolation, with subsequent genetic drift and differing selection pressures lead to genetic divergence (Balloux & Lugon-Moulin, 2002; Koenig, 2002; Vanderwerf *et al.*, 2010) that may result in allopatric speciation on separate islands (Orr & Smith, 1998; Glor *et al.*, 2004). The geological histories of archipelagos play an important role in shaping the biogeography of islands. When islands are of different ages, island colonisation often moves from older to younger islands, as seen on Hawaii, where the islands of decreasing age have formed a line as the oceanic crust has moved over a crustal hot-spot (Hormiga *et al.*, 2003; Rubinoff, 2008). On the Galapagos, although the islands are in clusters rather than a linear series, the direction of colonisation for a series of taxa has generally gone from older to younger islands (Parent *et al.*, 2008; Benavides *et al.*, 2009). The last glacial maximum (LGM) 18,000 years ago; when the sea level was 120 metres or more lower than today (Fairbanks, 1989) has also affected the biogeography of many islands. The lowered sea level exposed some land bridges and eliminated or decreased the over-water distance between some island land masses, and this facilitated dispersal between islands. Consequently, current populations of species on islands that were connected by Pleistocene land bridges often show decreased genetic distance compared to those on islands that have remained isolated, and this pattern can be detected for both volant and non-volant species (Heaney *et al.*, 2005).

The Melanesian Solomon Archipelago is situated in the South West Pacific and spans two countries, Papua New Guinea (PNG), which has political claim on the island of Bougainville, and the Solomon Islands, to which the remaining islands belong (Fig. 1). The islands have complex geological histories that create excellent conditions for assessment of biogeography, ecology and evolution. The islands of the Solomon Archipelago have never been connected to neighbouring continents, but emerged from the ocean as a consequence of a collision between the Indian and Pacific Plates (Hall, 2002). All of the biota on the archipelago is therefore a result of speciation through founder events rather than vicariance. The various islands of the archipelago have different geological compositions, origins and emergence times, but the specific historical details are largely unknown. A current hypothesis is that the Western Province is the youngest part of the archipelago and is a result of volcanic activity during the Pliocene and Pleistocene. The islands of the Western province are therefore likely to have emerged less than five million years ago (Petterson *et al.*, 1999). The earlier emergence times of the remaining islands are largely uncertain, but are estimated to range from 30-90 MYA (Petterson *et al.*, 1999; Hall, 2002). Several islands of the archipelago were probably connected to each other during the LGM (Fig. 1). Bougainville, Choiseul, Isabel and Ngela were joined and Guadalcanal would have been either connected to the same landmass or separated from it by a narrow channel. At the same time the Western Province was represented probably by two major islands (Mayr & Diamond, 1976; Mayr & Diamond, 2001). Makira and Malaita are separated from each other and from the rest of the archipelago by deeper channels and probably have been isolated for a substantial geological time (Mayr & Diamond, 2001) (Fig. 1).

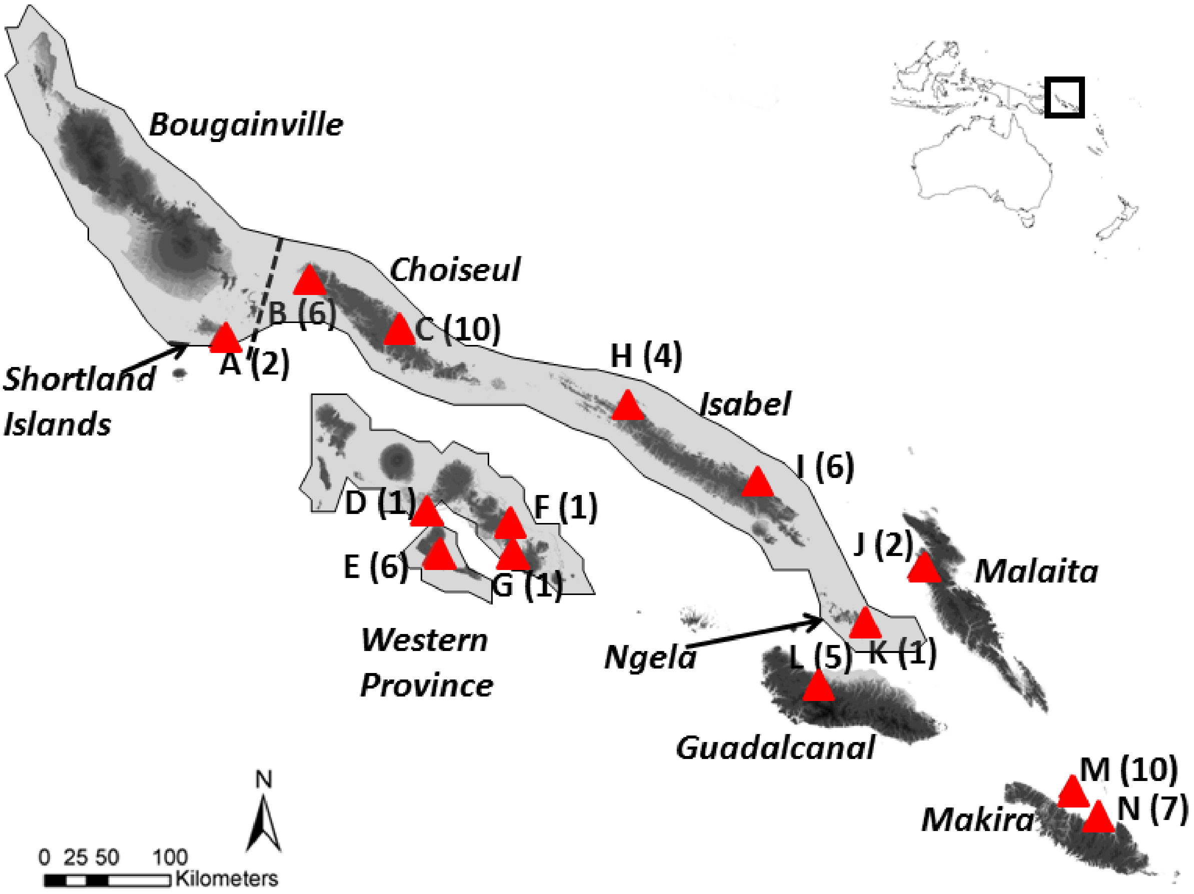

Figure 1: The Solomon Archipelago. The broken line represents the sub-species boundary according to McCoy (2006). Sample locations are indicated by red triangles. Letters represent the sampling locations and numbers in brackets represent the number of samples collected from each location. Shaded areas represent probable Pleistocene land bridges. Bougainville, Choiseul, Isabel and Ngela were joined in a single landmass, whilst the Western Province was separated into two larger islands.

The historical colonisation patterns of the archipelago are important in order to understand the origins of the Pacific biota and are now being explored with molecular genetic methods on a number of taxonomic groups, (e.g. birds: Filardi & Smith (2005); Smith and Filardi (2007); bats: Pulvers and Colgan (2007) and reptiles: Austin *et al.* (2010)). Pulvers and Colgan (2007) described a close association between genetic lineages of bats on the Solomon Archipelago and phylogenetic relationships predicted from presumed Pleistocene landmass conformations. A similar pattern was found for birds (Smith & Filardi, 2007). Both bats and birds can fly, thus making inter-island dispersal quite likely. Non-volant animals like reptiles and amphibians generally have slower dispersal rates which could result in smaller scale genetic structure and higher local population differentiation (Hughes *et al.*, 1997). Currently, no extensive biogeographic study of Solomon Archipelago reptiles (or amphibians) based on molecular phylogenetics has been conducted.

The prehensile tailed skink lizard, *Corucia zebrata* (Gray, 1855) is an ecologically and evolutionary unique reptile endemic to the archipelago. Belonging to the *Egernia* group (Gardner *et al.*, 2008), a largely Australian lineage of skinks, *C. zebrata* is the sister lineage to the remainder of the group and molecular clock estimates suggest that it has been separated from the other seven genera in the group for about 26 MYA (Skinner *et al.*, 2011). This divergence then post-dates the period over which the Solomon Archipelago is believed to have emerged (Hall, 2002). *Corucia*, has traditionally been considered monotypic, with its single species represented by two geographically separated sub-species, *C. z. zebrata* to the east and *C. z. alfredschmidti* to the west (Kőhler, 1997). The exact geographic location of the sub-species boundary is uncertain, but is likely to lie between the Shortlands/Bougainville and Choiseul (Kőhler, 1997; McCoy, 2006) (Fig. 1). The sub-species hypothesis is based on morphological characteristics and has not been tested using molecular genetic methods (Kőhler, 1997). *Corucia z. alfredschmidti* is described as being smaller, having a slightly different colour pattern and with a different number of parietal scales (7 vs usually 5 on *C. z. zebrata*) compared to *Corucia z. zebrata* (Kőhler, 1997). It is worth examining the divergence between the two sub-species as often in reptiles, subspecies are found to be separate species (Burbrink *et al.*, 2000).

Corucia gives birth to live young and may reach a weight of over 1000 g. The combination of large size, a prehensile tail and a nocturnal, herbivorous and arboreal nature makes it ecologically unique among the Scincidae (McCoy, 2006; Hagen & Bull, 2011) and the species has come to symbolise the remarkable ecotype of the Solomon Islands. This large skink is therefore an appropriate species on which to focus the first molecular systematic study of a Solomon Archipelago reptile.

We used molecular genetic tools to elucidate the phylogeography of *Corucia.* Our hypothesis was that that the geographic distance between islands and the sea level changes due to the LGM have affected the phylogeography of the species. Specifically, we made the following predictions: 1) The genetic divergences derived from both mitochondrial and nuclear data will be lower between populations on islands that were connected by Pleistocene land-bridges than between those on islands that have remained isolated. 2) The genetic distance between populations will increase with geographic distance between islands (Isolation by Distance (Wright, 1943)), reflecting that gene flow decreases with increasing distance between populations and that selection and genetic drift due to environmental conditions differs increasingly with increasing geographic distance between populations.

Additionally, we wished: i) to make inferences on the geographical origin and dispersal pattern of *Corucia* within the Solomon Archipelago, and ii) to use molecular clock calibrations and knowledge of the geological history to estimate the dates of the colonization events for the different islands across the archipelago, and iii) provide data to clarify the systematic status of the two sub-species of *C. zebrata*.

Materials and Methods

We collected samples from 44 *C. zebrata* caught in the Solomon Islands between July 2007 and May 2008. Sample locations and sample sizes are indicated on Fig. 1. The lizards were captured by hand and their GPS location and island of origin were recorded. The outer 1 mm of ten scales were cut from each individual using sharp scissors and preserved in 70% ethanol. Tissue samples from another 17 individuals from the frozen tissue collections of the Australian and South Australian Museums were also included. The sample locations for all 61 samples are listed in Appendix 1. The 61 samples included representatives from all major island groups with the exception of Bougainville, which is PNG territory. In the study period we could not get appropriate research permits and were not able to enter the island for sampling purposes. Three other species of the *Egernia* group (*Egernia depressa, E. saxatilis* and *Lissolepis coventryi*) were used as outgroups for the analyses of the mitochondrial data. Outgroup details are listed in Appendix 1.

DNA extraction, PCR amplification and sequencing

DNA was extracted from scales or liver using a Puregene™ DNA Isolation Tissue Kit, D–7000A (Gentra Systems), following the manufacturer's instructions. We amplified two sections of the mitochondrial genome (*ND2* and *ND4*) and four nuclear loci (*rhodopsin* intron 4, *β-fibrinogen* intron 7, *AKAP9* coding for amino acid positions 482-688 in the human gene and *PTPN12* coding for amino acid positions 298-497 in the human gene. See Table 1 for primer sequences and PCR conditions for each locus.

Table 1: Sequences, PCR conditions and references for the six loci used.

Locus	Reference	Ta (ºC)	Forward (5'-3')	Reverse (5'-3')
NADH dehydrogenase subunit 2 (ND2)	Primers designed by author	55	GCACTMATYATTRCAACWTGACA	TTGGGTGTTTAGCTGTTA
NADH dehydrogenase subunit 4 (ND4)	Primers designed by author	54	TCAATAAAACTATGCTACCC	AATTAGCAGTTCTTTGTGTG
Rhodopsin intron 4	Primers designed by author	54	GCTCAGCCATCTACAATCC	CATGATCATACAGTTACGG
B-fibrinogen intron 7	Primers designed by author	62	TGGACAACATCAAGCCCAC	GGTGAACTCCTTGCCAAAG
AKAP9	Townsend *et al*. (2008)	58	AGCARATWGTRCAAATGAARCARGA	TCHAGYTTYTCCATRAGTTCTGTTG
PTPN12	Townsend *et al*. (2008)	58	AGTTGCCTTGTWGAAGGRGATGC	CTRGCAATKGACATYGGYAATAC

The two mitochondrial markers that we used have been informative for previous phylogeographic studies in reptiles (e.g Gardner *et al.* (2008)). The two non-coding nuclear loci *rhodopsin* (Bossuyt & Milinkovitch, 2000; Page, 2000; Austin *et al.*, 2010) and *ß-fibrinogen* (Giannasi *et al.*, 2001) are known to show intra-specific variation in a number of taxa. The two nuclear protein encoding genes were reported by Townsend (2008) to be among the most variable nuclear genes screened across a range of squamate reptile species, and therefore likely to be informative in phylogeographic studies.

The PCR reaction mixtures were prepared using AmpliTaq Gold (Applied Biosystems) following the manufacturer's recommendations, with approximately 100 ng template DNA, 10mM total of each dNTP, 0.2 μM of each primer, 0.5 μg/μL BSA and 4 mM MgCl, in a final volume of 25 μL. The following PCR cycle was used: 94º, 5 min; (94º, 45 sec; Ta, 45 sec; 72º, 1 min) × 38; 72º, 10 min. The annealing temperatures (Ta) were adjusted to the optimum for each primer (Table 1). The PCR reactions were purified using a MultiScreen vacuum manifold (Millipore) following the manufacturer's protocol. The sequencing reactions were prepared with BigDye Terminator v3.1 Cycle sequencing kit (Applied Biosystems), following the manufacturer's protocol. The samples were sequenced in both directions. Electrophoresis was carried out on an ABI PRISM 3730 Analyser (Applied Biosystems). The sequences were edited using the ContigExpress function in Vector NTI v10 (Invitrogen). For the nuclear genes we used parsimony to manually resolve alleles in heterozygous individuals. In individuals where phase could not be resolved, PCR products were cloned and several clones sequenced for each product. We used a StrataClone PCR Cloning Kit (Agilent Technologies), following the manufacturer's recommendations. The clones were sequenced as described above.

Data analysis

The sequences were aligned in Geneious v4.5.5 (Drummond *et al.*, 2008) using the MUSCLE alignment algorithm (Edgar, 2004) via a plugin. The coding sequences were translated to protein sequences in ContigExpress to verify that the reading frame was not disrupted by premature stop codons or deletions, as a further check of sequence quality and locus identity. We used DNAsp v5 (Librado & Rozas, 2009) to characterize within-population genetic diversity, to test for recombination, to estimate haplotype diversity (Nei, 1987) and to characterize statistical properties of the different sequences. Haplotype networks were generated in TCS v1.21 (Clement *et al.*, 2000). This program is very sensitive to unequal sequence length and missing data, hence alignments were cropped to equal length prior to analysis. We used the corrected AIC score (Akaike, 1979) in Mr.ModelTest v2.3 (Nylander,

2004) to select the appropriate models of nucleotide substitution for each locus and data partition.

Bayesian analyses with mitochondrial data were carried out in MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001). Due to the low number of variable sites and hence limited information we chose to make the lowest possible number of partitions; thus concatenating the two mitochondrial loci and combining the 1st and 2nd codon positions. The following partitions and models were used: 1st and 2nd (GTR+I+G), 3rd (GTR+G) and tRNA (HKY+I). The analysis was run twice with 20,000,000 MCMC iterations, and sampled every 1000 generation. The reliability of the analyses was verified in Tracer v1.5, where the trace files for the posterior probabilities, prior, likelihood and the nucleotide models can be examined and unreliable parameters are indicated by the program (Rambaut & Drummond, 2007). The two runs were combined and the first 4000 trees were discarded as burn-in. We used TreeAnnotator v1.5.4 (Rambaut & Drummond, 2008) to generate a maximum clade credibility consensus tree. FigTree v1.2.2 (Rambaut, 2008) was used to edit the consensus tree. Outgroups represented a significant challenge as it is thought that the nearest related taxa to *Corucia* have has been separated from *Corucia* for more than 26 million years, and therefore placement of the root in the ingroup is probably imprecise (Piller & Bart, 2009). Due to reported issues regarding the MrBayes scale bar (Brown *et al.*, 2010), we verified the scale against trees generated in BayesPhylogenies (Pagel & Meade, 2004) and Neighbor joining trees generated in MEGA v.3.1 (Tamura *et al.*, 2007).

We quantified the divergence between different islands for the concatenated mitochondrial data set using the Tamura and Nei distance method with 10,000 permutations in ARLEQUIN v3.1 (Excoffier *et al.*, 2005). Due to a sample size of one, the population from Ngela was omitted from this analysis. The larger sample sizes and multiple collecting locations for Choiseul and Isabel allowed for an additional pair-wise comparison between the eastern and western sampling areas on each of these islands. We analysed all nuclear loci together, in ARLEQUIN v3.1 using the Tamura and Nei distance method. We calculated the average F_{st} value for all loci and determined the significance level using 10,000 random permutations. Individuals with more than three nuclear loci missing were omitted from the analysis.

A Mantel test for isolation by distance (IBD) using the mitochondrial data was carried out using the Isolation by Distance Web Service v3.16 (Jensen *et al.*, 2005). We performed two separate analyses wherein the geographic distances were defined as: 1) the distance (km) separating the actual sample locations, and 2) the minimum span of open water between the different islands from where the samples were taken.

We attempted to date the splits between the different *Corucia* clades using BEAST v1.5.4. The partitions and models of evolution were identical to the above described MrBayes analysis. We selected a UPGMA generated starting tree with a coalescent constant size tree prior and a relaxed clock with uncorrelated log-normal site model. The priors were specified with the following calibrations: Emergence of the Western Province provides an upper limit for colonization of this part of the archipelago and was set to maximum 3 MYA with a uniform distribution. The split between the ingroup and the outgroups has been estimated to be 26 MYA (+/- 5.1) (Skinner *et al.*, 2011). The MCMC chain was run for 10,000,000 generations, sampling every 1000 trees. After examining the posterior probabilities in Tracer, we discarded the first 1000 trees as burn-in. A maximum clade credibility consensus tree was generated from the remaining 9,000 trees using TreeAnnotator. The consensus tree was edited in FigTree.

Results

Recombination and statistical properties of the loci

Recombination was detected at a number of sites in *β-fibrinogen* as can be seen in the haplotype network (Fig. 5). No other locus was affected by recombination. There were large differences among loci in the number of variable sites (Table 2). As expected, the mitochondrial sequences were the most informative, followed by nuclear non-coding and nuclear coding loci. Different numbers of haplotypes were identified using TCS and DNAsp. This is due to how the two programmes treat missing data.

Table 2: Sequence information and variability of genetic markers. N indicates the number of samples sequenced, alignment length in bp with alignment length after removal of recombinant section in brackets, the number of variable sites, number of parsimony informative (PI) sites, the number of variable sites per bp for each locus, indels listed by length in bp, number of haplotypes observed and the haplotype diversity. For haplotypes observed, the numbers outside brackets refer to the number of haplotypes identified by DNAsp whilst the numbers in brackets refer to the number of haplotypes identified by TCS.

	ND2/ND4	***AKAP9***	***β-fibrinogen***	***Rhodopsin***	***PTPN12***
N	57	27	33	61	41
Length (bp)	1698	742	594	871	672
Vari. sites	144	3	7	12	7
PI sites	124	2	5	8	5
Var. sites %	0.085	0.003	0.012	0.014	0.009
Indels	0	0	9	0	0
# haplotypes	33	3 (4)	8 (13)	11	6 (7)
Haplotype diversity	0.972	0.211	0.758	0.516	0.460

Phylogenetic relationships between island populations

A maximum clade credibility tree from the 36,000 trees generated from the mitochondrial data using the two combined runs of Bayesian inference is presented in Fig. 2. There is weak support in the deeper nodes in the tree whilst the support towards the tips is very strong for some clades. The deepest split within the ingroup is between populations from Makira/Malaita and those from the remainder of the sampled islands. Apart from populations from Choiseul and the Western Province, all islands were reciprocally monophyletic with strong support. The Western Province sample was nested within the Choiseul clade, and the support for this placement was strong. Additionally, there was reciprocal monophyly for the eastern (location I) and western (location H) sampling locations on Isabel, with a support of 0.7 (support not shown on tree). As for the two sampling locations on Choiseul, the western (B) sampling location is monophyletic but is nested among the east (C) Choiseul haplotypes, and is therefore paraphyletic with both west Choiseul and the Western Province. The sample from Ngela was placed as a sister group to the samples from Isabel, whilst Makira and Malaita were sister clades. The samples from Shortland Islands were somewhat divergent from the remainder but nested close to the samples from Isabel. The trace files for both runs indicated that these analyses were reliable (data not shown).

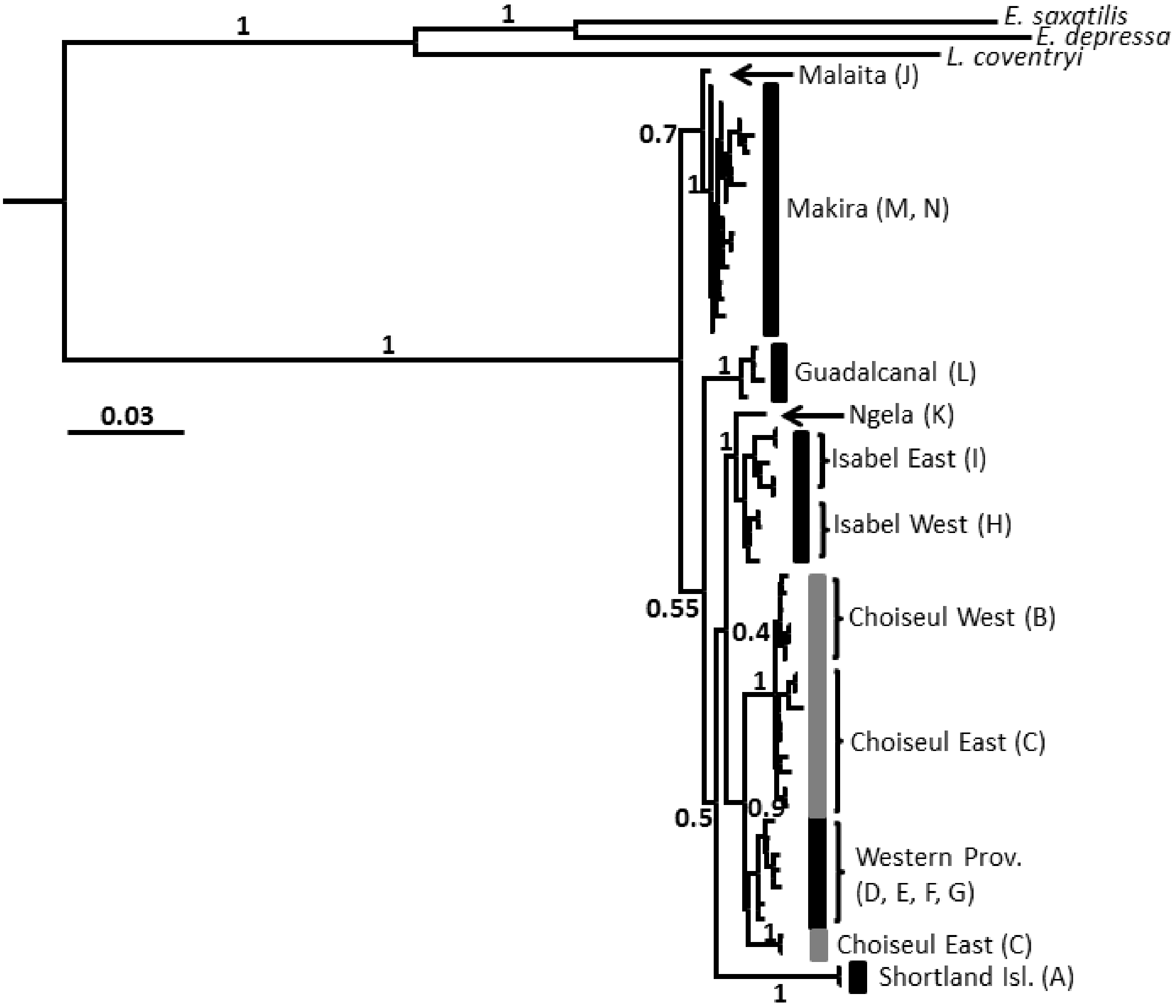

Figure 2: Maximum clade credibility consensus tree from 36,000 trees after two combined MrBayes runs of 20,000,000 MCMC iterations each. Letters in brackets refer to the sampling locations on Fig. 1. Numbers represent the posterior probabilities.

Inter-island genetic divergence

Genetic distances generated in ARLEQUIN from the concatenated mitochondrial data are presented in Table 3A. Pair-wise F_{st} values between the sample from the Shortland Islands and those from the other islands in the archipelago (minimum of 0.866, mean = 0.93, SE = 0.02) were typically higher than values derived from comparisons among the other islands (mean = 0.8, SE = 0.02). Choiseul and Isabel had a pair-wise F_{st} of 0.709; which was marginally lower than the pair wise F_{st} values for those with Guadalcanal and Malaita (range 0.734 - 0.770). The sample from Western Province had lower pair wise F_{st} values with samples from Choiseul (0.678) and Isabel (0.744) than with samples from the remainder of the eastern islands (0.84 - 0.924). The pair-wise F_{st} value for Makira and the other islands was the second highest after the Shortland Islands (mean 0.88, SE = 0.03). For the respective sampling locations within the islands of Choiseul and Isabel (not included in Table 3), the pair-wise F_{st} values were 0.42 (*p*

<< 0.001) between the eastern and western sampling site of Choiseul and 0.62 (*p* << 0.001) between the eastern and western sampling site of Isabel. Only the pair-wise value between samples from Malaita and the Shortland Island was below the 0.05 level of significance.

Table 3: A) Pair-wise genetic distances between islands in the Solomon Archipelago for *C. zebrata* using the combined *ND2* and *ND4* sequences and B) the combined *APAK9, β-fibrinogen*, *PTPN12,* and *rhodopsin* sequences. Values below the diagonal are F_{st} values; values above diagonal are the *p*-values of the respective F_{st} values. Bold values were significant at an α of 0.05.

A	Makira	Malaita	Guadal-canal	Isabel	Choiseul	Western Prov.	Shortland Islands
Makira	*	**0.009**	**0.000**	**0.000**	**0.000**	**0.000**	**0.008**
Malaita	**0.762**	*	**0.047**	**0.018**	**0.004**	**0.025**	0.342
Guadalcanal	**0.903**	**0.797**	*	**0.000**	**0.000**	**0.001**	**0.046**
Isabel	**0.871**	**0.777**	**0.753**	*	**0.000**	**0.000**	**0.018**
Choiseul	**0.85**	**0.734**	**0.77**	**0.709**	*	**0.000**	**0.006**
Western Prov.	**0.924**	**0.87**	**0.84**	**0.744**	**0.678**	*	**0.03**
Shortland Is.	**0.973**	1.00	**0.917**	**0.866**	**0.873**	**0.93**	*
B							
Makira	*	0.999	0.999	**0.014**	**0.002**	0.07	0.154
Malaita	0.000	*	0.999	0.999	0.21	0.999	0.999
Guadalcanal	0.000	0.000	*	0.999	**0.045**	0.499	0.396
Isabel	**0.01**	-0.187	-0.064	*	**0.005**	0.357	0.846
Choiseul	**0.463**	0.291	**0.375**	**0.29**	*	**0.005**	**0.05**
Western Prov.	0.139	-0.086	0.04	0.021	**0.443**	*	0.234
Shortland Is.	0.297	-0.091	0.111	-0.064	**0.33**	0.08	*

Pairwise genetic distances for nuclear data are presented in Table 3B and were often negative (effectively zero). The sample from Choiseul had the overall highest pair-wise F_{st} values (minimum of 0.29, mean = 0.37, SE = 0.03) compared to those that involved comparisons among samples from the other islands (mean = 0.04, SE = 0.03). Makira had an overall pair-wise F_{st} value of 0.15 (SE = 0.08) with other islands, while the Shortland Islands had an overall pair-wise F_{st} value of 0.11 (SE = 0.07). The Western Province sample had higher pair wise F_{st} values with Choiseul (0.443) than with Isabel (0.021) and with samples from the remainder of the eastern islands (0 - 0.139). Choiseul and Isabel had a pair-wise F_{st} of 0.29, which was the highest observed value for Isabel and the lowest observed value for Choiseul. Less than half of the pair-wise F_{st} values in Table 3B were significant at an α of 0.05.

Isolation by distance

A Mantel test did not detect a significant isolation by distance from the combined mitochondrial data ($r^2 = 0.04$; $p = 0.12$) when analysed with the geographic distance between sample locations. However, when geographic distance was set as the minimum span of open water between sampled islands, there was significant isolation by distance ($r^2 = 0.19$; $p = 0.045$; Fig. 3).

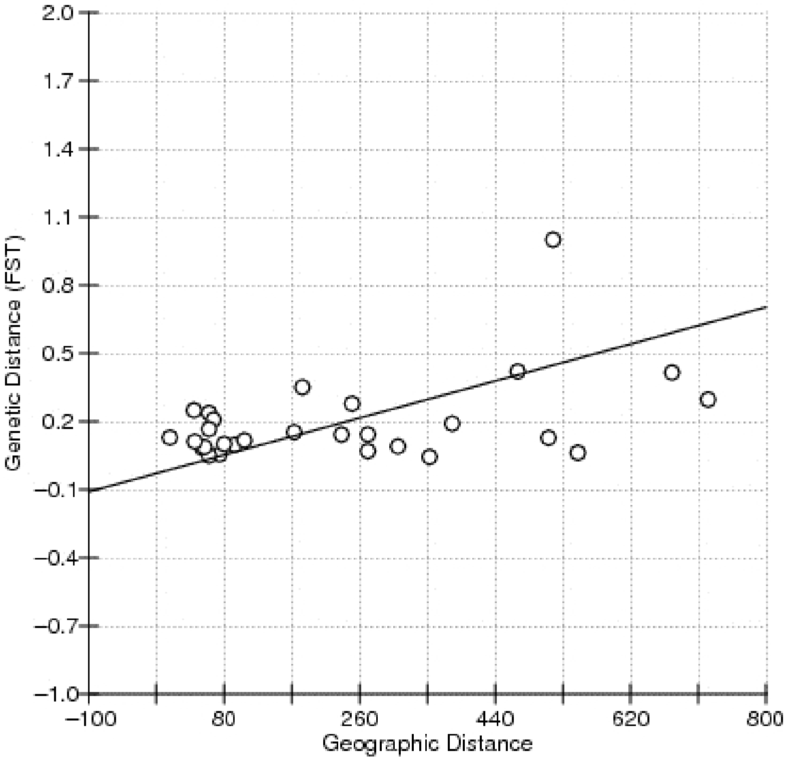

Figure 3: A Mantel test carried out on mitochondrial data with genetic distances set as the minimum span of open water between islands. Geographic distance (km) is on the x-axis and genetic distance (F_{st}) is on the y-axis.

Haplotype networks

A haplotype network for the mitochondrial loci is presented in Fig. 4. Haplotype networks for the protein encoding loci *AKAP9* and *PTPN12* are presented in Fig. 5A and B, and for the nuclear non-coding loci *rhodopsin* and *β-fibrinogen* in Fig. 5C and 5D.

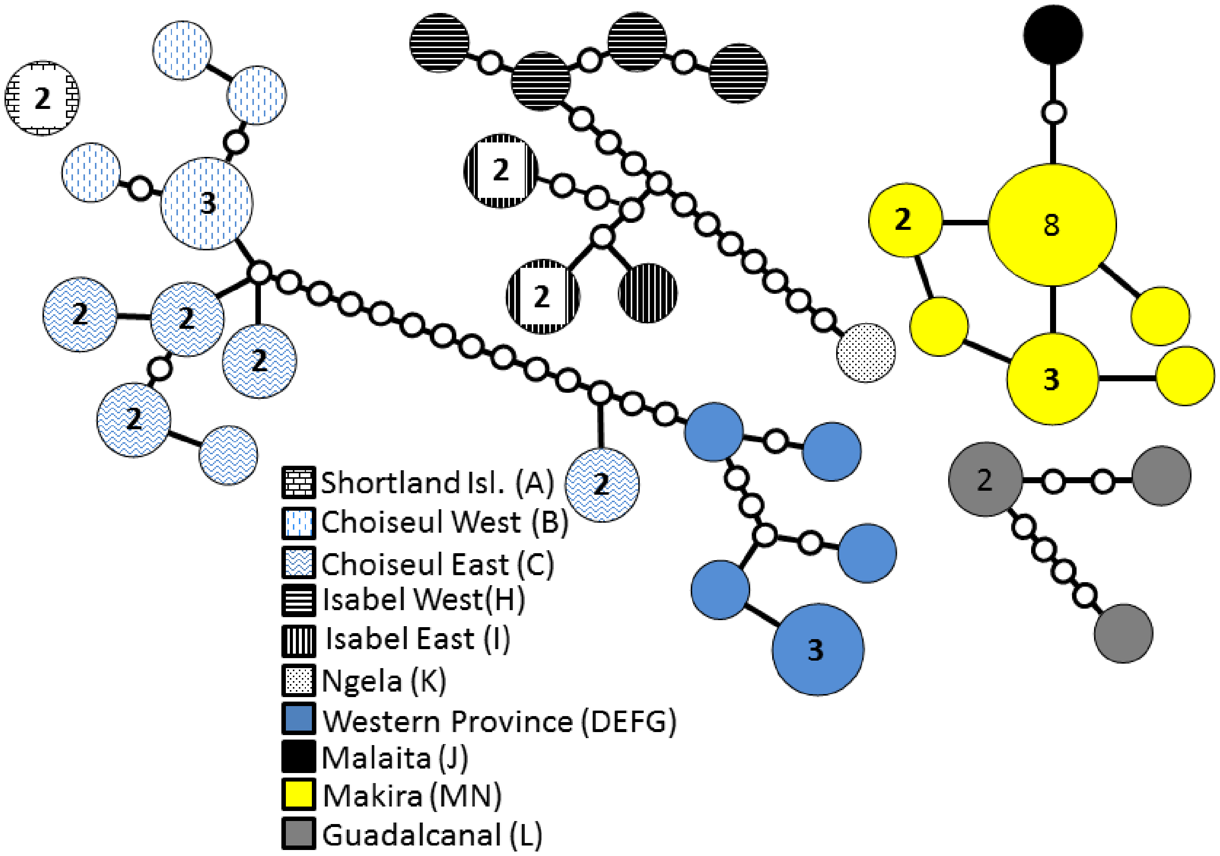

Figure 4: Haplotype networks for the mitochondrial *ND2* and *ND4* loci. Numbers inside circles indicate the number of individuals with that haplotype. Circles without numbers are haplotypes represented by only one individual. Letters in brackets refer to the sample locations on Fig. 1. A branch represents a single substitution and empty circles represent hypothetical haplotypes. Isabel constituted a separate network, as did Guadalcanal and the Shortland Island. Malaita was joined in a separate network with Makira. Choiseul and the Western Province were joined in a separate network.

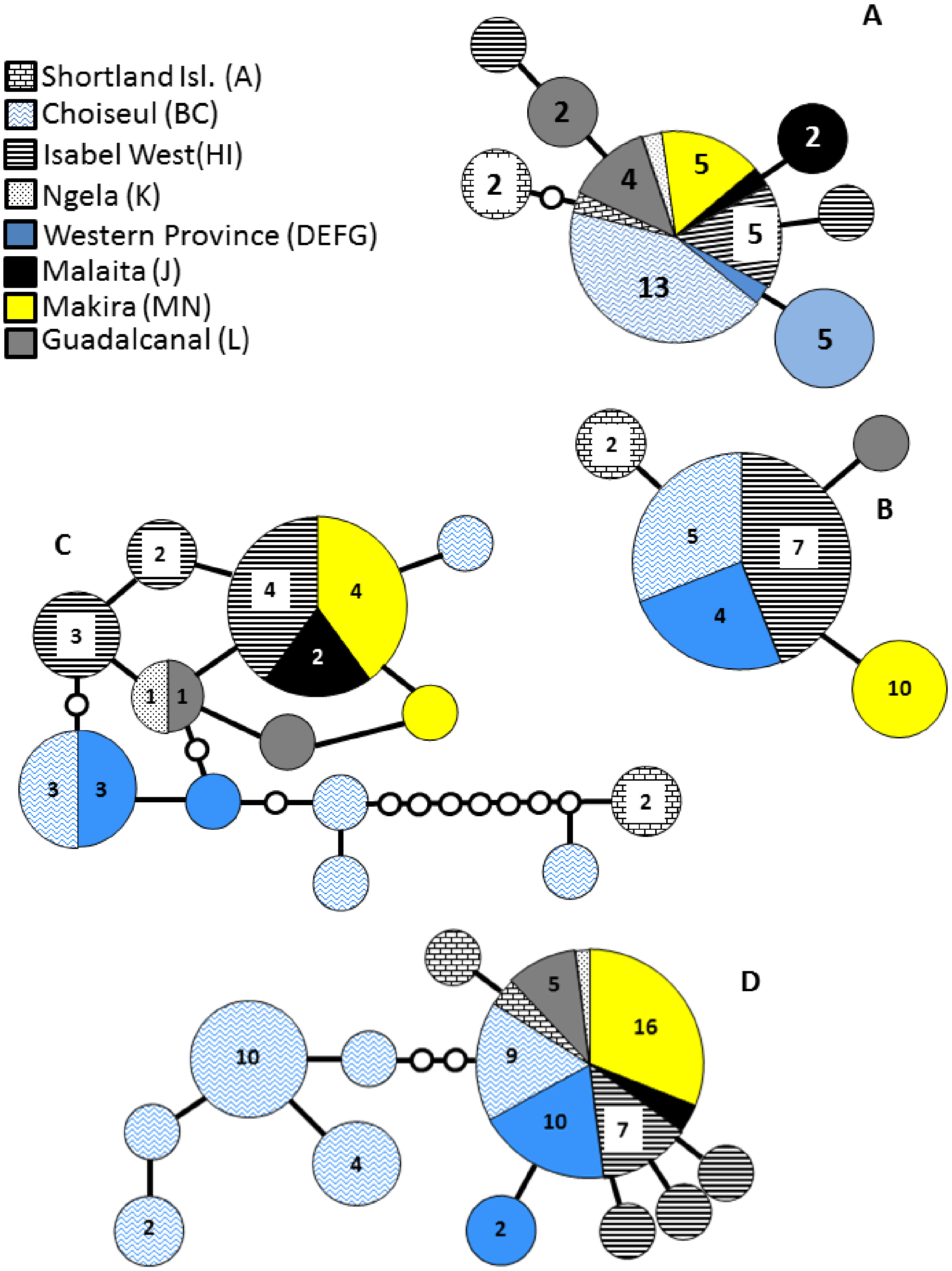

Figure 5: Haplotype networks for (A) *PTPN12*, (B) *AKAP9*, (C) *β-fibrinogen* and (D) *rhodopsin*. Numbers inside circles indicate the number of individuals with that haplotype. Circles without numbers are haplotypes represented by only one individual. Letters in brackets refer to the sample locations on Fig. 1. A branch represents a single substitution and empty circles represent hypothetical haplotypes. For *PTPN12*, the Shortland Islands, Ngela and the Western Province are represented by one individual each in the pie chart. For *rhodopsin*, Ngela is represented by one individual and the Shortland Islands and Malaita are represented by two.

For the mitochondrial loci, the separate islands constituted separate networks with the exception of Malaita which was included in a network with Makira, and the Western Province which was included in a network with Choiseul. The mitochondrial networks suggested that the haplotypes in the Western Province originated from Choiseul and that the samples from Malaita were genetically close to those from Makira. For the nuclear loci on the other hand, there was no concordance between haplotype and island origin as the most frequent allele in *rhodopsin* and *PTPN12* was present on all islands. There were few haplotypes present in *AKAP9*. Here, one haplotype was restricted to the Shortland Islands and another haplotype was restricted to Isabel, but there was no further sorting. The multiple linkages in *β-fibrinogen* reflected the recombination detected at that locus, and involve alleles from all the sampled islands except the Shortland Islands.

Dating of colonization events within the Solomon Islands

A consensus tree of the 9,000 trees generated from the mitochondrial data using BEAST is presented in Fig. 6. Our attempt to derive a date for the colonization events of *C. zebrata* using priors with specified divergence times produced a tree topology which was somewhat different from the tree presented in Fig. 4. The samples were placed in the same clades in both trees, but the placement of the different clades in relation to each other was not concordant in the two trees. This was reflected in the support for the respective nodes, which in both trees was low in the deeper nodes and high towards the tips. When examining the trace files, it was apparent that the reliability of the analysis was compromised, as many of the parameters were outside the recommended range (data not shown). The analysis suggested that *C. zebrata* colonized the Solomon Archipelago within the last 1 - 4 million years, and that some islands may have been colonized within the last 100,000 – 500,000 years, although no inferences about the site and timing of initial colonisation and subsequent spread could be made. The large confidence intervals for the out group and the root to the in group (Fig. 6), indicated the large degree of uncertainty in relation to the dating of the nodes.

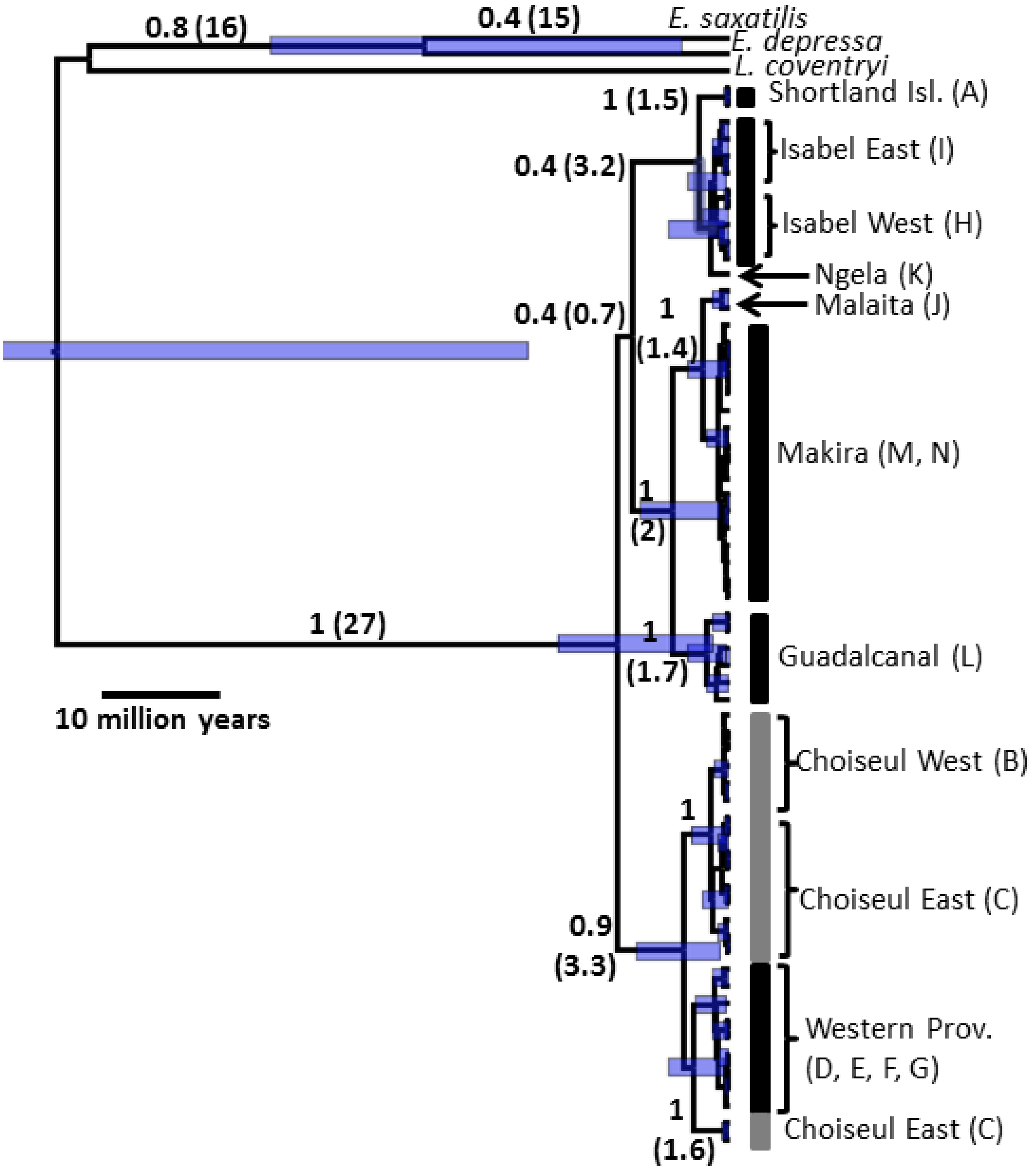

Figure 6: Maximum clade credibility consensus trees from 9,000 trees sampled during 10,000,000 MCMC iterations in BEAST. Numbers outside of brackets represent the posterior probabilities and numbers inside brackets are MYA since divergence. Support was weak for the deeper nodes in the ingroup and strong for the separate clades towards the tips. The archipelago has been colonised during the last 1-4 million years. Blue bars are confidence intervals for the most important nodes.

Discussion

Our results from analysis of mitochondrial and nuclear nucleotide sequence data from the scincid lizard *C. zebrata* did not support the hypothesis that intraspecific genetic variation is explained by Pleistocene land bridges. We found that lizards on islands isolated throughout the glacial cycles were indeed divergent in their mitochondrial sequences. However there were patterns pertaining to recent dispersal and colonisation of isolated but geologically younger islands as well as genetic divergence of islands previously connected by Pleistocene land-bridges that were not congruent with the above hypothesis. These incongruent patterns are described further below. The genetic distances for mitochondrial loci and geographic distances between islands partly supported the hypothesis that genetic divergence has resulted from isolation by distance, with populations more divergent if their islands are further apart.

Genetic distance and mitochondrial reciprocal monophyly in relation to Pleistocene land-bridges

The Pleistocene landbridge hypothesis predicts reduced genetic distance between islands connected during the LGM and higher genetic distance between islands that remained isolated during the LGM. Thus this hypothesis predicts that populations on Makira and Malaita should have the highest pair-wise F_{st} values, both to each other and to populations on other islands, whilst the F_{st} value between populations on Choiseul and Isabel should be low. Our results only partly supported those predictions in that the samples from the isolated island of Makira were highly divergent. However, the divergence of samples from Malaita was comparable to those from the remainder of the central islands of the archipelago. A low sample size for Malaita meant that the F_{st} values from this island were largely non-significant and results must therefore be interpreted with caution. Although samples from the previously connected islands of Choiseul and Isabel showed somewhat lower genetic divergence (F_{st} = 0.709, as opposed to means of 0.8 for Isabel and all other islands and 0.781 for Choiseul and all other islands) they were at the same time significantly different from each other, with a high F_{st} value and contained different strongly supported clades (see Fig. 4 and Table 3). We therefore rejected the hypothesis that Pleistocene land bridges can explain much of the intraspecific variation found in *C. zebrata*. This pattern differed from the pattern reported for *Melonycteris* fruit bats by (Pulvers & Colgan, 2007), where the current biogeographic regions were best explained by geographic conditions during the LGM, and where no genetic differences were detected between animals inhabiting islands previously connected by land bridges. Similarly, for a number of bird taxa, (Smith & Filardi, 2007) found patterns of low or no genetic variation between Isabel and Choiseul, and greater divergence for populations on historically isolated islands, again suggesting the importance of Pleistocene landbridges for birds. It is not known if the Pleistocene habitat between the islands of Bougainville, Choiseul, Isabel and Ngela was suitable for *C. zebrata* or whether the landbridge habitats supported a vegetation matrix that would encourage dispersal to more appropriate habitat during the last LGM. It is plausible that habitat unsuitable for *C. zebrata* may have allowed easier dispersal for volant animals than for large lizards. The fact that the extreme ends of Choiseul and Isabel represent distinct populations of *C. zebrata* (Figs. 2 and 4) suggests that the species infrequently disperses over distances such as the length of Choiseul or Isabel. Our study has therefore highlighted the important fact that biogeographic regions and processes for some island species cannot be directly extrapolated from taxa with differing dispersal abilities.

Bougainville, Choiseul, Isabel and Ngela were joined by land bridges during the LGM (see Fig. 1). The Shortland Islands are situated within less than 8 km of Bougainville and were likely to have been included in the larger landmass of Greater Bukida, together with Bougainville, Choiseul, Isabel and Ngela. Indeed, the lowest pair-wise F_{st} values for samples from the Shortland Islands were between the islands of Choiseul (0.88) and Isabel (0.87), thus suggesting that the animals on the Shortland Islands are genetically closer to Choiseul and Isabel than to animals from the rest of the archipelago. This is congruent with expectations based on geological data. According to McCoy (2006), *Corucia* on the Shortland Islands belong to *C. z. alfredschmidti,* however our results were somewhat ambiguous in this respect: the samples from the Shortland Islands were divergent, but still nested within the remainder of the samples (Fig. 4) and with only slightly higher F_{st} values than those for Makira (Table 3). Hybridisation between *C. z. alfredschmidti* and *C. c. zebrata* on the Shortland Islands is a possibility. Ultimately inclusion of samples from Bougainville is required to provide a robust molecular genetic test of the systematic status of *C. z. alfredschmidti* and *C. z. zebrata.* In regard to how the morphologies of the sampled animals correspond to the sub-species descriptions, some measurements were made, but as these were done in the field with active animals, they can not be considered reliable for taxonomic purposes, and with sample sizes too small to make statistically rigorous conclusions. Some observations on colour morpholoy are worth mentioning, as much of the description of *C. z. alfredschmidti* is based on this. No such information exist for the animals from the western side of Choiseul (location B) and the eastern side of Isabel (location I), as well as Malaita (location J) as these were not handled during the sampling periods between July 2007 and May 2008. Animals (N = 2) on the Shorland Islands were bright green, with darker stripes and black sclera, thereby fitting the description of *C. z. alfredschmidti*. Parietal scales were not recorded. With respect to lizards on Choiseul (location C), these resembled the colour description of *C. z. alfredschmidti*, with a brighter green and black sclera. Lizards were found to have white sclera on the remainder of the archipelago, and with animals in the east (Makira, locations M, N) displaying brown body colour with less prominent banding, although green, banded animals were encountered also on Makira. Black sclera on animals from Choiseul was not expected and may indicate that this trait varies over a geographic cline.

Most islands were reciprocally monophyletic for mitochondrial DNA, which indicated that episodes of gene-flow between the islands have been rare and that the genetic lineages on separate islands are probably the result of single colonisation events (or single sources of colonisation) on the respective islands. There was not enough information in the data set to resolve the relationships among the individual clades on separate islands, reflected by the low support for the deeper splits in the trees. Nuclear haplotypes shared between different islands (Fig. 5) indicated incomplete lineage sorting, which may produce gene trees that are either not congruent with species trees (Moran & Kornfield, 1993), or incongruent with the true phylogeographic pattern of *C. zebrata*, in the case of the current study. Low F_{st} values for nuclear loci compared to mitochondrial loci were consistent with incomplete lineage sorting. The more structured data from mitochondrial loci are likely a result of the smaller effective population size and thus shorter coalescence time for the mitochondrial genome. Reciprocal monophyly is expected to require considerably more time to develop for nuclear loci due to the larger effective population size for the nuclear genome (Nei, 1987), sometimes up to several million years (Hudson & Turelli, 2003). The smaller effective population size for the mitochondrial genome will lead to stronger effects of demographic stochasticity. These effects can be enhanced during founding events by small population sizes and by multiple impregnations of founding females. The latter will be an important factor amongst age-structured species with overlapping generations such as *C. zebrata*. In light of the relatively recent divergence of *C. zebrata* (Fig. 6) incomplete lineage sorting on nuclear loci was not surprising, and suggested that gene flow between islands has happened too recently to allow for complete sorting of nuclear loci, yet rarely enough to allow for reciprocal sorting of mitochondrial haplotypes (with the exception of Choiseul and the Western Province). Theoretically, this pattern could also be explained by male-biased dispersal, however given that gene flow in *C. zebrata* is likely to be the result of stochastic events (see below), this explanation is improbable. On the other hand, the opposing signal between the nuclear and mitochondrial pair-wise F_{st} values was unexpected. It is plausible that these different results were a product of the highly variable sample size between the different sampling locations, and Makira, Choiseul and Isabel were the locations from which the highest number of samples were derived. This was reflected in the significance for the different pair-wise F_{st} values, where locations with small sample sizes were generally above the 0.05 α level. The greater sample size will also have uncovered more haplotypes and thus greater genetic divergence in these locations. However, this can not explain the shared alleles and therefore lack of lineage sorting. Our study indicated that mitochondrial loci are the most useful molecular markers for assessing the phylogenetic relationships between *C. zebrata* populations on separate islands. Nuclear loci were included in the analysis as evolutionary relationships inferred from one gene tree may be insufficient for estimations of the true species tree (Moore, 1995). However in this case the divergences between the different populations were too shallow for nuclear loci to yield useful phylogenetic information. This study indicated that different loci that evolve at different evolutionary rates can give contrasting results, thus highlighting the importance of choosing the appropriate molecular marker in studies of phylogenetics.

Genetic distance in relation to geographic distance

The size of the dispersal barrier (i.e. the geographic distance of open water between islands) appeared to explain approximately 20% of the intraspecific variation in *C. zebrata*. Much of this is likely to be driven by the genetic distance and geographic isolation of the Shortland Island samples. Although there is some support for the hypothesis that Isolation by Distance has driven variation, this is unlikely to be a strong factor behind the overall observed pattern.

Colonization history and dating of colonisation events within the Solomon Islands

The Western Province has been isolated throughout its existence but is situated in geographical proximity to Choiseul, and separated from it by ~60 km of open water. The low F_{st} value between the Western Province and Choiseul was in concordance both with the tree topologies in Fig. 2, where the Western Province was nested within Choiseul and with the haplotype network in Fig. 4. This suggested that the Western Province was colonised by animals from the geologically much older Choiseul. Given the young age of the Western Province, a direction of colonisation events from the nearby Choiseul to the Western Province is concordant with expectations based on geological data. With the exception of this Western Province example, it was difficult to infer a dispersal pattern among any other of the islands from our phylogenetic reconstruction (Figs. 2, 6). Pulvers and Colgan (2007) argued that fruit bats (*Melonycteris*) most likely colonized the Solomon Archipelago from east to west, starting at Makira, as bats on Makira appear most basal in the *Melonycteris* phylogeny. Pulvers and Colgan (2007) did not acquire samples from Bougainville. When a mitochondrial phylogeny of *C. zebrata* is reconstructed without samples from the Shortland Islands (data not shown), the tree topology resembles that of *Melonycteris* in Pulvers and Colgan (2007). A more complete sampling regime may thus alter the topology of the tree and it is plausible that a similar effect may occur if Bougainville samples were included in the *Melonycteris* phylogeny. A rapid and recent radiation across the archipelago with subsequent isolation could explain the results of the current study. This hypothesis is supported by results from dating using BEAST, which suggested that *C. zebrata* colonised the archipelago during the last 1 - 4 million years (Fig. 6). This is surprising given that *C. zebrata* diverged from the other genera of the *Egernia* group approximately 26 MYA, and one would therefore expect a deeper divergence for some clades.

It is possible that Bougainville is the site of initial colonisation and that the species was restricted to this island for several million years prior to dispersal to other islands. Another scincid taxon *Tribolonotus* radiated primarily from Bougainville and it is plausible that Bougainville (which is close to the larger land mass of New Guinea) is the source of a number taxa that have spread to the eastern islands of the Solomon Archipelago (Austin *et al.*, 2010). Bougainville must be included amongst the *C. zebrata* sample locations in order to test this hypothesis.

Dispersal ability and mechanism of colonisation

Corucia zebrata has probably colonized across the Solomon Archipelago by over-water dispersal on flotsam. This kind of colonisation event was observed in the Caribbean archipelago where a number of *Iguana iguana* occupied an extensive raft of uprooted trees and arrived at an island where the species previously did not occur. The raft probably entered the sea during a previous hurricane (Censky *et al.*, 1998). This observation by Censky *et al.* (1998) documented how island colonisation by reptiles is possible; if there can be successful establishment of the populations after arrival to the new location. Over-water dispersal on flotsam is assumed to be the mechanism behind the *Anolis* radiation in the Caribbean (Schoener & Schoener, 1984; Glor *et al.*, 2005), as well as radiation of reptiles of the Mexican Revillagige Islands (Brattstrom, 1990). The Solomon Islands regularly experiences tropical storms (cyclones), which frequently cause large land slides (pers. obs.) that may generate large rafts when washed into the sea. *Corucia zebrata* is a canopy dwelling species, and one tree may be inhabited by several lizards (Hagen and Bull, 2011). Rafts comprising large trees may therefore contain a number of *C. zebrata,* thus facilitating successful establishment upon arrival. The herbivorous diet of the species would prolong survival of individuals on rafts that contained tree foliage. Phylogenetic comparisons with other species, such as the native frog *Litoria lutea*, with a lower tolerance for exposure to sea water, fewer on-raft feeding opportunities and thus lower dispersal ability than *C. zebrata,* would give a more complete understanding of the historical biogeography of the Solomon Archipelago.

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research was carried out with permits from the Flinders University Animal Welfare Committee and the Solomon Islands Department of Education.

CHAPTER 3

Hanging about in Trees: Population Genetic Structure of the Prehensile Tailed Lizard, *Corucia zebrata*

This chapter has been submitted to Wildlife Research
as of 3 Jan 2011 and is in review, as of 21 Jan 2011

A *C. zebrata* from Ngela Island

Abstract

Context. The spatial genetic structure of a population is an important ecological parameter that can be affected by geographical barriers and social organisation. The scincid lizard *Corucia zebrata* belongs to the highly social *Egernia* group of Australian lizards and lives in lowland rainforest canopies in the Solomon Islands. *Corucia* is an evolutionary distinct and monotypic genus and represents a species for which very few ecological parameters are known.

Aims. We explored the small scale population genetic structure of a population of *C. zebrata* with the aim of uncovering previously unknown ecological parameters pertaining to population structure and potential social organisation.

Methods. We investigated the genetic structure from a sample of 51 lizards captured in a 900 ha study plot within a larger area of continuous rainforest on Ugi Island, using Bayesian assignment analysis and pair-wise relatedness between individual lizards derived from eight polymorphic DNA microsatellite loci.

Key results. We found the connectivity within the population to be high. Additionally, there was ambiguous evidence for social associations of family groups: on the one hand we found adults and related offspring in groups sharing day-time canopy refuges and on the other hand we found no evidence that pairs of lizards captured closer together were more related than were pairs of lizards captured further apart.

Conclusions. Our data suggest there may be some short-term family association in this species; however more studies, perhaps with captive animals, are required to determine the presence of social behaviour in *C. zebrata.*

Implications. Importantly, potential social adaptations in this species do not affect the overall genetic structure of the population.

Introduction

Spatial genetic structure, e.g. the non-random distribution of genotypes, may arise either from reduced gene flow due to natural or anthropologically induced physical discontinuities in the habitat (Peakall *et al.*, 2003; Moore *et al.*, 2008b; Smith *et al.*, 2009), or from social organisation. Social organisation, such as the clustering of related individuals, has been reported to induce genetic subdivision in mammals (Storz, 1999) and birds (Painter *et al.*, 2000; Temple *et al.*, 2006; Berg *et al.*, 2009). We used spatial genetic structure to investigate population structure and to explore possible social organisation in an elusive canopy dwelling scincid lizard, *Corucia zebrata*, a sister taxon to the *Egernia* group of largely social Australian lizards.

In some lizard species genetically related individuals are more clustered than by chance, apparently by the stable aggregation of family groups (Gardner, 1999; Gardner *et al.*, 2001; Chapple & Keogh, 2006). Stable social groupings of lizards have been reported as isolated and phylogenetically independent cases in several lineages of lizards, including agamids (Panov & Zykova, 1993) and iguanids (Lemos-Espinal *et al.*, 1997). However an unusually high proportion of species within the largely Australian *Egernia* group of skinks form stable aggregations of related individuals that defend heterogeneously aggregated or limited resources (see Chapple (2003) for review). In these viviparous and generally large skinks, social aggregations can contain a breeding pair and one or more cohorts of their offspring and may be stable over multiple years (Duffield & Bull, 2002). Populations containing these groups show a high degree of genetic structure and strong inverse relationships between genetic and geographic distance (Gardner, 1999; Gardner *et al.*, 2001; Fuller *et al.*, 2005). All well documented reports of social structure in the *Egernia* group stem from species that spend most of their time close to ground level and are relatively easy to observe directly. Most have been based on molecular genetic verification of relatedness within visually identified social aggregations that have been followed for a number of years (Duffield & Bull, 2002; O'Connor & Shine, 2003; Chapple & Keogh, 2005; 2006). Studies of more elusive species in less accessible habitats face a range of challenges when the study species cannot be easily observed or captured. Molecular approaches may in such instances yield reliable data on species life history and population structure whilst reducing the need for logistically difficult and time consuming field studies.

The prehensile tailed lizard - *Corucia zebrata* (family: Scincidae) is an *Egernia* group species (Gardner *et al.*, 2008a), but separated from the other genera in the group approximately 26 MYA (Skinner *et al.*, 2011). *Corucia* is a monotypic genus endemic to the Solomon Archipelago, where it inhabits the canopy of rainforests (McCoy, 2006). The conservation status for the species is unknown but harvest for the international pet market has been assumed to affect a number of populations (McCoy, 2006). *Corucia zebrata* is also a popular protein source for people in the Solomon Islands (pers. obs.) and widespread logging affects the species' habitat (Wein & Chatterton, 2005). *Corucia zebrata* reaches an adult weight of over 1000 g and is one of the largest species of skinks. It is unique among the Scincidae for the combination of being folivorous, nocturnal and arboreal (McCoy, 2006). The species has strong home range fidelity (Hagen & Bull, 2011) and anecdotal information about individuals emerging from shared refugia has suggested that the species may behave socially (McCoy, 2006). A prediction from that suggestion is for spatial genetic structuring even in a homogenous habitat with no barriers to gene-flow. However, beyond the anecdotes, neither the incidence of social aggregations, nor the persistence of those groups, nor the degree of relatedness within groups has been established.

The features that make the species ecologically and evolutionarily unique also make it challenging to study. It is difficult to detect (Hagen and Bull, 2011), and due to its folivorous diet cannot easily be caught in food baited traps. Rainforest canopies are largely inaccessible to field workers, and visual location is hard, particularly at night, when *C. zebrata* is most active. The use of traditional field techniques for behavioural studies is therefore not an easily attainable strategy for *C. zebrata.* Instead, we made use of microsatellite DNA as an alternative and cost effective way of assessing the genetic structure of a *C. zebrata* population on Ugi Island in the Solomon Archipelago. With this study, we aimed to 1) aid conservation management of *C. zebrata* in the Solomon Islands by expanding the limited knowledge of *C. zebrata* ecology, and 2) expand the broader knowledge of the distribution of sociality within the *Egernia* group. *Egernia* sociality has previously been studied in depth on a limited number of species. Information about the distribution of sociality in a wider range of *Egernia* group taxa may allow for inferences about the origin of sociality within this group (Gardner *et al*., 2008a).

The rainforest habitat in our study area appeared uniform with no obvious barriers to gene flow, thus we predicted that all individuals belonged to the same population. In regard to potential social organisation, we considered two alternative predictions. Either this species may be similar to many other species in the *Egernia* group with stable family groups that generate strong genetic structuring within populations and where related individuals share refugia. In that case we expected to find that animals found sharing refugia should be related, and more generally, that there should be an inverse correlation between genetic relatedness among pairs of individuals and their distance apart. Alternatively, if there is no social structuring, we expected individuals to be randomly mixed over the entire population with respect to their genotypes.

Methods and Materials

We sampled 51 lizards in a 900 ha area of mature, closed canopy rainforest on the island of Ugi (10°14'S; 161°45'E; Fig. 1) in the Solomon Islands from October 7 – 10, 2007 and from April 17 to May 24, 2008. Ugi Island is about 50 km^2 in area and is located approximately 8 km north of the larger island, Makira (see Fig. 1).

The island has not been subject to commercial clear cut logging, but there has been selective subsistence level logging and clearing of patches of up to 1000 m^2 of forest for local agriculture. Also some mature trees have been removed for village construction. However, the canopy has for the most part remained closed and supports a sparse understory. The habitat is uniform across the island, which lacks geographic features such as large rivers or elevated land that could act as barriers to gene flow for the lizards. The study area represents about 20% of the continuous, suitable *C. zebrata* habitat on the island.

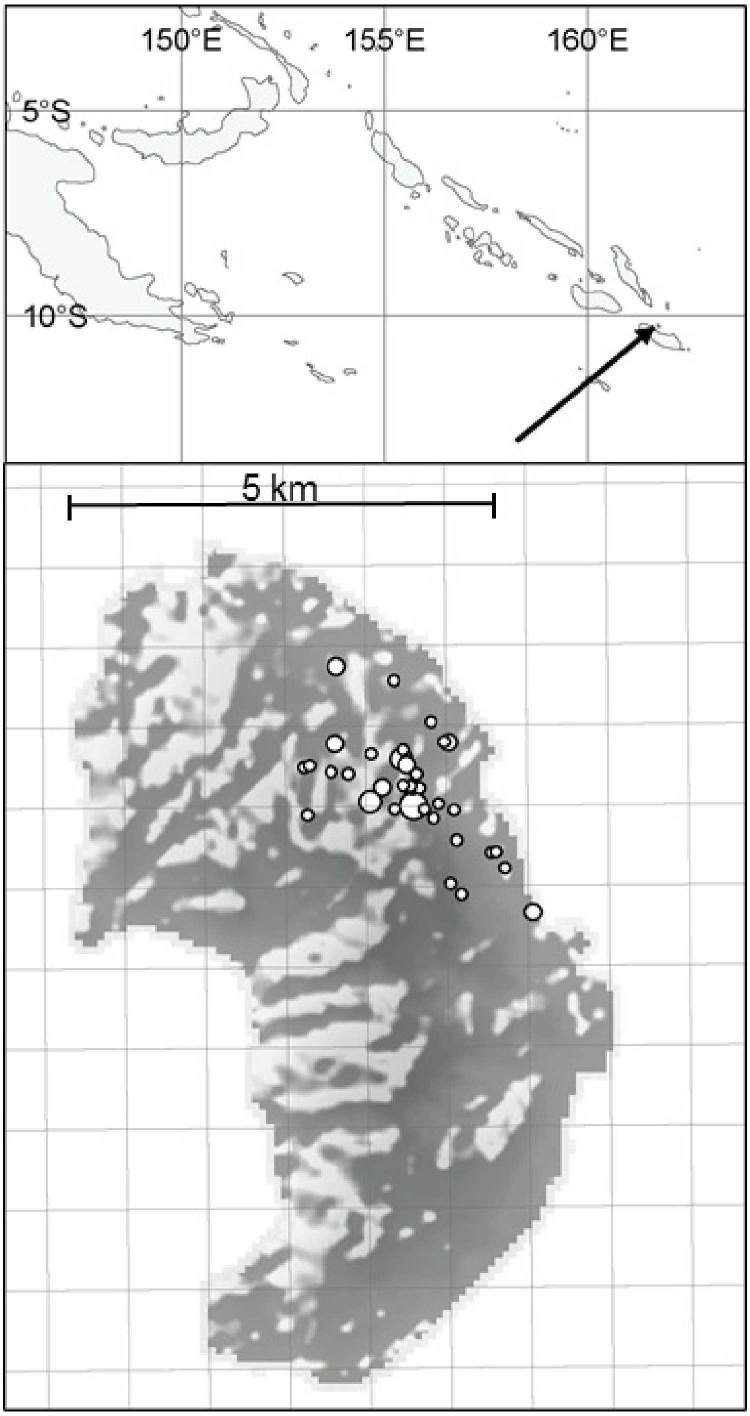


Figure 1: Map of Ugi Island. The position of Ugi within the Solomon Islands is indicated with an arrow. Circles indicate the sampling locations. The size of the circles indicates the number of lizards sampled at a given location.

The lizards were captured by hand from the trunk (at canopy level, about 20 m above the ground) or in the canopy of tall forest trees and strangler figs, and their GPS locations were recorded. Where multiple lizards were observed together, all detected individuals were recorded even when they could not all be captured. The outer 1 mm of ten scales was cut from each sampled individual using sharp scissors and preserved in 70% ethanol for DNA analysis. The lizards were then released back into their trees. For analysis we assumed that all lizards caught in the canopy or on the trunk of a single tree were together (0 m apart), and the distance between lizards caught in different trees was taken as the distance between the trunks of those trees.

Determination of juvenile vs. adults

There is no current information about the size at which *C. zebrata* reaches sexual maturity in the wild. However breeders of captive *C. zebrata* have reported that both males and females reach sexual maturity at about 250 mm snout to vent length (SVL) (Celeste Satter pers. comm., 2010). Although rates of growth and development may differ between field and captive populations, for this study we considered animals longer than 250 mm SVL to be adults.

DNA extraction and PCR amplification

DNA from five scales of each animal was extracted using a Puregene™ DNA Isolation Tissue Kit, D–7000A (Gentra Systems), following the manufacturer's instructions. We genotyped the 51 individuals at 11 microsatellite loci: *3HDZ84*, *3HDZ116*, *3HDZ151*, *3HDZ157*, *3HDZ159*, *3HDZ194*, *3HDZ453*, *3HDZ519*, *3HDZ818*, *3HDZ864A* and TrL1 (Brenneman *et al*., 2007; Gardner *et al*., 2008b). The primers derived from *C. zebrata* (loci named with *3HDZ* prefix) were fluorescent labeled using the method described in Schuelke (2000), where the sequence specific forward primer has an M13 tail at the 5'end. We followed the procedure in Schuelke (2000) with a 10 μL reaction volume, the only exceptions being a 1/8 relationship between the forward and reverse primers and a 20 minute final extension. The PCR conditions are listed in Table 1. The direct labeled primer pair (*TrL1*) was amplified under the conditions described in Gardner *et al.* (2008b). The reactions were multi-plexed post PCR according to the volumes described in Table 1. After multi-plexing, the samples were made up to a total volume of 100 μl with TE and cleaned using a MultiScreen vacuum manifold (Millipore) following the manufacturer's recommendations, before finally being eluted in 30 μl TE.

An ABI3730 capillary electrophoresis DNA analyser (Applied Biosystems) was used to genotype the samples. A fluorescently labeled size standard [GS500 (-250) LIZ] (Applied Biosystems) was run with each sample. The alleles were scored using GENEMAPPER version 3.7 software (Applied Biosystems). Genotyping error was controlled for by re-amplifying and genotyping eight samples from each 96-well plate (hence 8/96 samples were run twice). Each 96 well plate also had a control sample with no DNA. Additionally, eight samples were repeated between plates. As we were unable to unambiguously genotype the *3HDZ157* and *3HDZ818* loci on the ABI3730 capillary DNA analyzer, they were visualized on a 5% denaturing acrylamide gel (Sigma-Aldrich) using a Gel-scan 2000 (Corbett Research). The samples were diluted 1/10 in

98% formamide, denatured and loaded on the gel together with a 50 bp increment 100 – 500 bp DNA ladder. Allelic states were determined by visual examination of the banding pattern. Accurate fragment sizes for the most common loci were determined on the ABI3730 capillary DNA analyzer during initial test runs.

Microsatellite data analysis

Genotyping error was estimated to be less than 3%. We used Micro-Checker 2.2.3 to test for null-alleles amongst the microsatellite markers (Van Oosterhout *et al.*, 2004). This analysis indicated that locus *3HZD546* displayed an excess of homozygotes for most allele sizes, a pattern that is likely to be caused by allele-dropout. That locus was omitted in subsequent analyses. Summary statistics and tests for deviation from Hardy-Weinberg (HW) equilibrium were carried out in GENALEX 6.0 (Peakall & Smouse, 2006) with a Bonferroni correction for multiple testing. Allele diversity ranged from 2 – 19 alleles per locus (mean 7.7; Table 1). Among the 10 loci that were tested, two loci deviated from HW equilibrium (*3HDZ194* and *3HDZ864A*), and were therefore not included in further analysis. We used GENEPOP (Raymond & Rousset, 1995) to test for linkage disequilibrium (LD), which was not detected between any of the remaining 8 loci which were all included in the final analyses.

Table 1: PCR conditions for the 10 microsatellites and post-PCR multiplexing of reactions. The reactions were multi-plexed into plex I or plex II. Primer sequence for TRL1 is found in (Gardner *et al*. 2008b), whilst the remaining sequences are from (Brenneman *et al*. 2007). Locus 3HDZ159 displayed an excess of heterozygotes and was excluded from further analyses. Summary statistics are presented for 51 *Coruzia zebrata* captured on Ugi Island. Loci that deviated from HW equilibrium are indicated with *.

Locus	Plex	M13-label	μl used	Repeat motif	Ta (°C)	Size range (bp)	Alleles	H_o	H_e
TrL1	I	Pet	4	$(AC)_{24}$	60	220-250	9	0.882	0.837
3HDZ84	I	Ned	6	$(CT)_{20}$	51	120-160	7	0.640	0.643
3HDZ116	I	Vic	2	$(GT)_{20}$	58	240-254	2	0.068	0.066
*3HDZ194**	I	Vic	4	$(CA)_{37}$	56	110-140	14	0.745	0.793
3HDZ519	I	Ned	4	$(TC)_{12}(AC)_{18}$	54	163-183	4	0.520	0.479
3HDZ151	II	Fam	4	$(CA)_{22}CG(CA)_{10}$	62	180-208	8	0.529	0.573
3HDZ453	II	Ned	7	$(TA)_{12}N(TATC)_{21}N(TA)_5$	59	191-231	19	0.878	0.910
*3HDZ86A**	II	Ned	7	$(CA)_{10}$	51	127-157	7	0.700	0.690
3HDZ818	N/A	Hex	N/A	$(GT)_7(GA)_5GC(GA)_2$	51	250-260	2	0.300	0.349
3HDZ157	N/A	Hex	N/A	$(CA)_{18}$	58	220-250	7	0.853	0.814

Population sub-structure

Two separate Bayesian analyses were performed to assess potential subdivision in the *C. zebrata* population on Ugi Island, GENELAND and STRUCTURE. GENELAND (Guillot *et al.*, 2005) incorporates spatial co-ordinates into the analysis, while STRUCTURE has an option to use no prior information about geographic sampling site (Pritchard *et al.*, 2000; Pritchard *et al.*, 2007). Both methods rely on loci in HW equilibrium and no LD. For GENELAND we carried out three runs of 1,000,000 MCMC iterations each at the following parameters: minimum number of K = 1, maximum number of K = 3, uncertainty of coordinates = 5 m, thinning = 100, burn-in = 200,000, allele frequencies as correlated, spatial model as true and null allele model as false. STRUCTURE was run with the following parameters: allele frequencies as correlated, the admixture model with no prior population information, a burn-in of 200,000 and a MCMC length of 1,000,000 iterations. We simulated the number of populations from $K = 1$ to $K = 3$ and performed five independent simulations of each K to check for consistency across runs. The mean posterior probabilities (Ln Pr (X|K)) from the five simulations were plotted against K to determine where the highest value of Ln Pr (X|K) occurred, which was considered the most likely K (Pritchard *et al.*, 2007).

Individual-level population structure

Lizards were assigned to the location of the tree in which they were captured. Pair-wise relatedness values for animals belonging to the same overall population were determined using Li's relatedness coefficient (Li *et al.*, 1993) in SPAGeDi version 1.2 (Hardy & Vekemans, 2002) with 10,000 random permutations. According to Li's coefficient, relatedness is expected to be 0.50 between parent and offspring or between full siblings, and 0.25 for half-siblings. Negative relatedness values refer to individuals being less related than the population average. Even though the relatedness between full siblings of unrelated parents is 0.5, the actual relatedness (unless they are monogametic twins) may vary from 0.374–0.617 due to Mendelian sampling during meiosis (Visscher *et al.*, 2006).

We tested for correlations between genetic relatedness and spatial distance between pairs of individuals, using samples of all individuals, only adults, and only female-juvenile pairs. We used a parametric approach where the relatedness-distance relationship was described by an exponential function with the parameters ρ_0 (relatedness at distance 0), ρ_∞ (relatedness at an infinite distance) and a scaling parameter l which indicates the spatial scaling of the relatedness between pairs of individuals (for more details, see Grøtan *et al.* (2005) and Engen *et al.* (2005)). The function was fitted to the observed data, and compared against 1000 curves that were based on random re-samplings of the data. A spatial structure in the relatedness (i.e. the fitted curves based on the true data) was considered significant if the observed line was outside the 95% confidence interval (defined as the 2.5% and 97.5% quantiles of the re-sampled curves). We also investigated the relatedness of individuals lizards found living together in the same tree.

Results

Captures

Among the 51 lizards sampled there were 26 males, 14 females and 11 juveniles. Lizards were captured from 35 different trees within the study area. From 25 trees only a single lizard was captured, although other lizards may have been present but undetected. Of the ten trees with more than one lizard, we captured a male and a female from three trees, and various combinations of adult males, adult females or adults (both males and females) with juveniles from seven trees (Table 2). For four groups we observed more lizards than we were able to capture (Table 2, groups 7-10).

Population sub-structure

GENELAND suggested no more than one genetic group in the sample population (data not shown). For STUCTURE, Ln Pr (X|K) for 1, 2 or 3 population were -982.84 (0.36), -984.4 (1.02) and -984.92 (1.62) with standard deviation in brackets. This indicated that all samples were likely to have come from the same genetic group.

Group structure and relatedness

In all of the comparisons we tried (all individuals, just adults, females and juveniles), the genetic relatedness among pairs of individuals did not change with distance. The predicted relationship between genetic relatedness and distance among pairs of individuals was within the borders of the 95% CI from the randomly re-sampled relationship (Fig. 2). Thus, there was no evidence for spatial structuring of the genetic relatedness of individuals. Also, the pair-wise relatedness values between individual lizards indicated that individuals related on a full-sib or parent – offspring equivalent were often separated by up to four km, which approximately spans the diameter of the study site (Fig. 2).

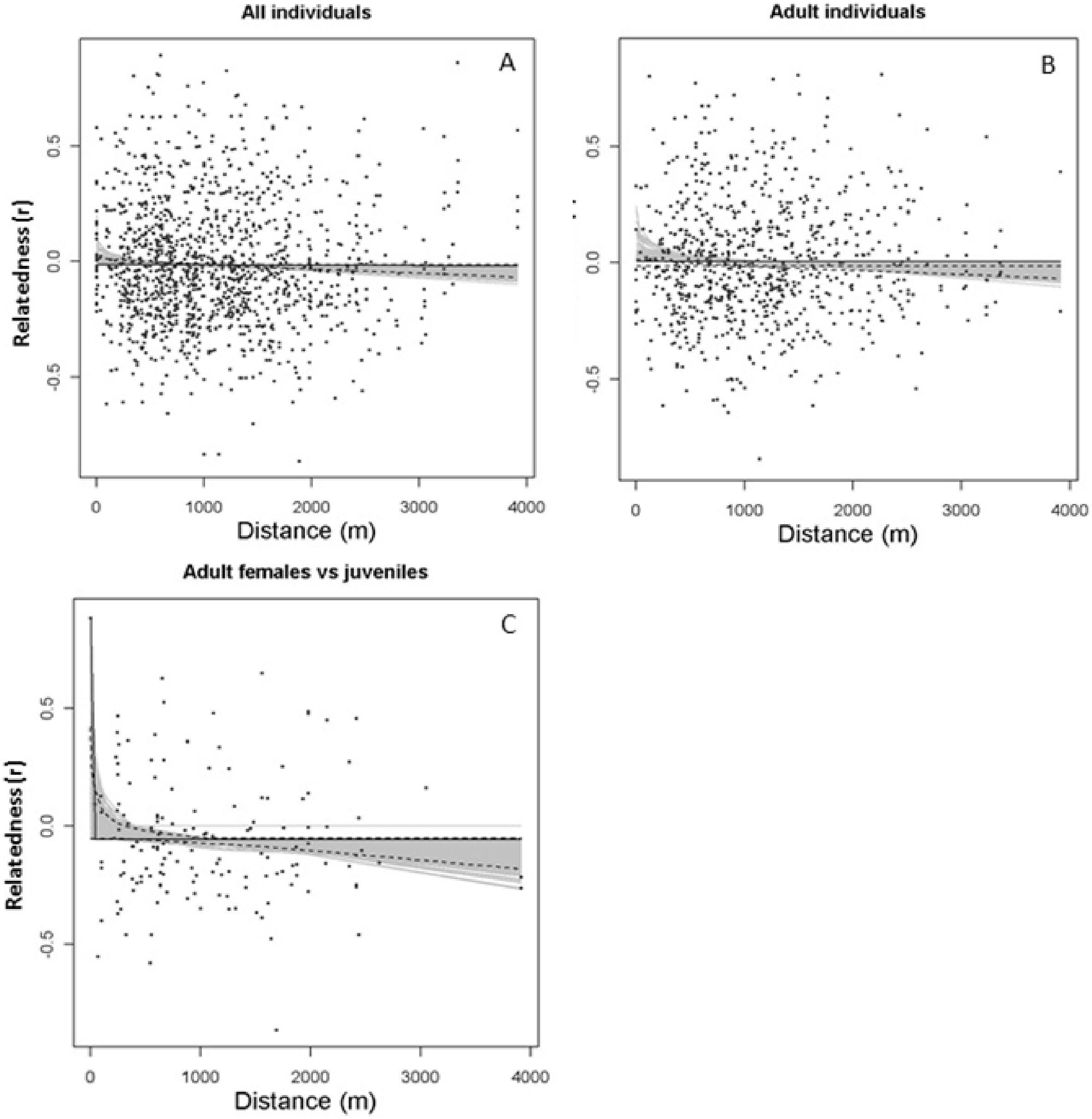
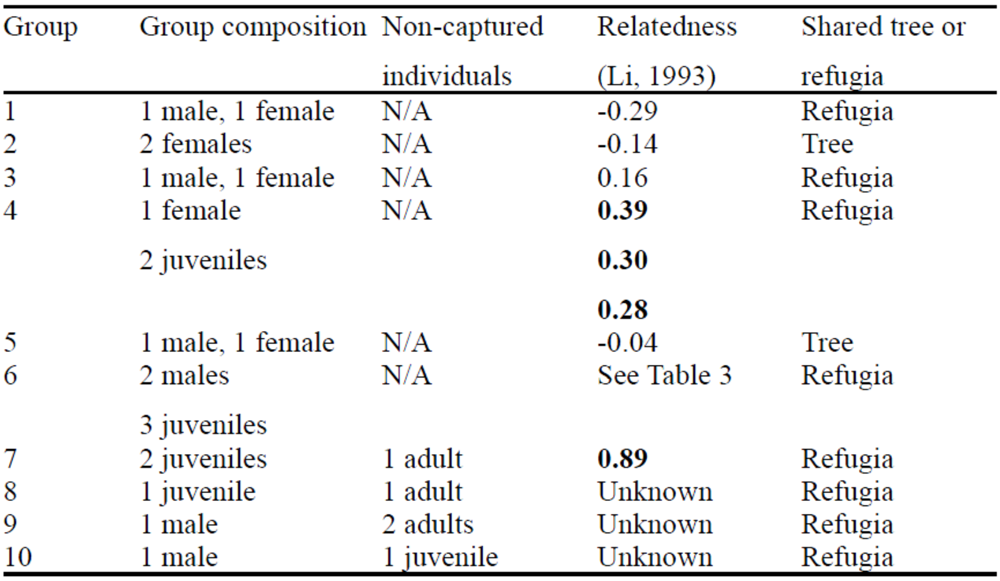


Figure 2: Pair-wise relatedness plotted against geographical distance between the pairs of observations. The solid lines indicate the predicted exponential relationship between relatedness and distance. Broken lines indicate the 95% interval. Grey lines represent relationship for randomised distribution of distance and relatedness based on the observations (N = 1000 resamplings), whereas the dashed lines gives the 95% confidence interval of the resamplings. Left upper panel (A) gives all individual paired, right upper panel (B) shows only adults, whereas lower panel (C) gives females paired with juveniles.

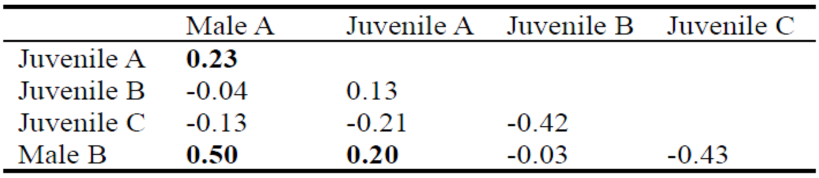
Nearly half of the lizards captured were not found near to any other detected lizards, although other lizards may have remained undetected in the same tree canopies. The 10 sampled groups were small, containing 2 – 5 detected individuals. Five of the groups contained juveniles and sub-adults, and eight of the groups contained individuals clustered in the same refuge (Table 2). Table 2 shows values of Li's genetic relatedness among lizards found sharing trees or crevice refuges. Three groups contained closely related lizards. Group 4 contained one adult female and two juveniles, all highly related to each other. This is probably a mother and two of her offspring. Group 6 included five lizards with two adult males and one juvenile all related to each other. Potentially, one male was the father of the juvenile and the other male could have been a brother (Table 3). Group 7 included two related juveniles who may have been siblings. An adult residing in the same crevice refuge was not captured.

Table 2: Group composition and kinship coefficient of cohabiting lizards in the ten groups located. Bold numbers represent animals that are related on approximate full sib or half sib level.



Group	Group composition	Non-captured individuals	Relatedness (Li, 1993)	Shared tree or refugia
1	1 male, 1 female	N/A	-0.29	Refugia
2	2 females	N/A	-0.14	Tree
3	1 male, 1 female	N/A	0.16	Refugia
4	1 female	N/A	**0.39**	Refugia
	2 juveniles		**0.30**	
			0.28	
5	1 male, 1 female	N/A	-0.04	Tree
6	2 males	N/A	See Table 3	Refugia
	3 juveniles			
7	2 juveniles	1 adult	**0.89**	Refugia
8	1 juvenile	1 adult	Unknown	Refugia
9	1 male	2 adults	Unknown	Refugia
10	1 male	1 juvenile	Unknown	Refugia

Table 3: Relatedness (Li, 1993) within group 6. Bold numbers represent animals that are related on approximate full sib or half sib level.



	Male A	Juvenile A	Juvenile B	Juvenile C
Juvenile A	**0.23**			
Juvenile B	-0.04	0.13		
Juvenile C	-0.13	-0.21	-0.42	
Male B	**0.50**	**0.20**	-0.03	-0.43

Discussion

Our study population occupied a part of a uniform habitat without any obvious geographic barriers to lizard dispersal. Thus its structure probably reflected the broader population on the island. All samples appeared to belong to the same genetic group, as shown by both the STRUCTURE and GENELAND analysis. Although this result was expected it was important to assess population sub-division which can arise from isolation by distance when the neighbourhood size is small (Wright, 1943; Pope *et al.*, 2006), or as a result of non-detected geographic barriers. This could have affected further relatedness analyses. The high connectivity in the population can be explained by the pair-wise relatedness between individual lizards: highly related pair of individuals were on some occasions separated by several km, which indicates frequent dispersal across the study area. The study area was relatively small compared to the inferred dispersal ability, thus it is possible that *C. zebrata* is able to disperse further than what we detected in this study.

In other social species of the *Egernia* group, individuals are typically found in stable social groups rather than alone (Duffield and Bull, 2002); and groups tend to consist of related individuals, often an adult breeding pair and one or more cohorts of related juveniles that remain within the parental home range (Gardner *et al.*, 2001; Stow *et al.*, 2001; Duffield & Bull, 2002; Chapple, 2003). Spatial autocorrelation carried out on populations of those species revealed relatedness decreasing with increasing geographic distance between individuals (Fuller *et al.*, 2005).

The data derived for *C. zebrata* from the current study provided equivocal evidence about social structure. On the one hand there was evidence of several groups of lizards sharing refuges or found in the canopy of the same tree during the day time when they are inactive. Because these are snapshot observations we cannot infer any stability of these groups, although radio-tracking data (Hagen and Bull, 2011) suggest that day to day movement of individual lizards is generally restricted to a single tree. Also we cannot make any estimate either of the size of groups or the frequency of group living versus solitary individuals, because of the difficulty of locating animals amongst the canopy foliage. The broader population analysis showed no significant trend for higher genetic relatedness among more closely spaced pairs of individuals (Fig. 2), as would be expected if related family members were clustered together. Together with the lack of spatial association between lizards that had overlapping home ranges as reported in Hagen and Bull (2011), this could indicate a lack of social adaptations in this species. However, among the groups that we did detect we observed five cases of adults and juveniles together, as would be expected if there was a family group structure. Two of these groups contained closely related adult and juvenile individuals, but for the other three possible family groups, we were unable to sample both the adults and juveniles. However, in one of those cases two juveniles were highly related, again consistent with a family group structure similar to that which has been reported for the social *Egernia* group species *Bellatorias major* (Osterwalder *et al.*, 2004). One explanation might be that unrelated males fathering offspring could hide a family related genetic structure. However, there was still no pattern when males were removed from the analysis and just pair-wise relatedness between females and juveniles was considered. Another possibility is that real genetic structure was obscured by lumping together two sets of samples taken six months apart, when substantial movement might have occurred. Our individual samples from each collection were too small for meaningful separate analyses.

Despite the lack of a negative correlation between genetic and geographic distance we can not rule out the occurrence of at least a short term family structure. A behavioural model that could explain the genetic data is that unrelated male and female adult lizards share tree canopy refuges in the daytime when they are inactive. Given the stable home ranges of this species (Hagen and Bull, 2011) it is possible that such associations may persist, at least over the short-term. Offspring may remain with their parents for a part of their early life (explaining the observations of associations of related adult and juvenile lizards in groups) but may then disperse widely while still in the juvenile age class (explaining the apparent lack of genetic clustering between females and juveniles in the overall data set). A test of this model will require more detailed field based sampling and observation, which is a challenging task in the natural habitat of *C. zebrata*, perhaps coupled with behavioural observations in captive populations. However, if such family groups exist, they do not affect the overall genetic structure of the population. Conservation managers should nevertheless be aware that lizards sharing refugia are highly likely to be closely related, despite the high degree of dispersal inferred by these results.

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CHAPTER 4

Home Ranges in the Trees: Radiotelemetery of the Prehensile Tailed Skink, *Corucia zebrata*

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An undisturbed *C. zebrata* in its natural habitat on Ugi Island (centre of photo).

Abstract

Corucia zebrata (Scincidae) is endemic to the Solomon Archipelago and widely distributed across the island group. *Corucia* is evolutionarily distinct and diverged from its nearest relatives about 30 MYA. Little is known about its life history, basic ecology, or behavior in the wild. We conducted a six-week study of movement patterns of *C. zebrata* on the island of Ugi to determine home-range sizes and overlap among conspecifics. Twenty-five lizards were fitted with radio transmitters and were followed for periods of 5–38 days. Telemetry results indicated that the average home range over the period studied was equivalent to the canopy of one tree. Radio-tagged individuals were located more often in the canopy than on the trunk of the tree, where humans typically search for the lizards. The home range is smaller than expected for a similar-sized herbivorous lizard occupying a terrestrial habitat, but the small home range is consistent with results from other arboreal animals. The study increased our knowledge of the behavior and habitat preferences of an ecologically unusual lizard species. We noted that conventional survey methods, searching tree trunk habitats, have low detection probability, an important consideration for further ecological studies of the species, in particular for the purpose of assessing its conservation status.

Introduction

Many species retain individual home ranges where they are familiar with the locations of feeding and refuge sites. The home range (HR) of an individual has been defined as the area that contains the requirements for its routine activities such as sheltering, foraging, and reproduction (Burt, 1943). The HR size of a species is often influenced by its foraging and metabolic requirements, and these are usually correlated with body size. Thus, large-bodied species need more food and tend to have larger HRs. This pattern is maintained in both mammals and birds (Harestad & Bunnell, 1979; Lindstedt *et al.*, 1986; Perry & Garland, 2000; Ottaviani *et al.*, 2006). Moreover, because more than 90% of energy is lost between trophic levels, carnivores are expected to need to forage for their energy requirements over larger HRs than equivalentsized herbivores, a prediction that is supported by many comparative studies (Harestad & Bunnell, 1979; Gittleman & Harvey, 1982; Ottaviani *et al.*, 2006). Specifically, Harvey & Clutton-Brock (1981) reported that, among 20 primate species, those with the most folivorous diets had the smallest HR. Within each trophic level, diet and foraging behavior affect metabolic needs, and these and other ecological factors also can influence HR size. For instance within herbivores, browsers have been found to have larger HRs than equivalent-sized grazers (Mysterud *et al.*, 2001). Additionally, HR size can be influenced by the complexity of the habitat, and Clutton-Brock

(1979) showed that arboreal primates that occupy three dimensional habitats have smaller HRs than equivalent-sized primates using more terrestrial and two-dimensional habitats.

The broad patterns of vertebrate HR size variation are maintained in lizards. A comprehensive study by Perry & Garland (2000) comparing 60 species of lizards showed body size to be a strong predictor of HR size and that carnivorous and insectivorous lizards had larger HR sizes than omnivores or herbivores of equivalent size. Perry and Garland (2000) also concluded that lizard species living on the ground had larger HRs than species occupying a three dimensional habitat, such as arboreal lizards occupying tree canopies. We examined whether a little known, arboreal but highly distinctive lizard, *Corucia zebrata* (Gray, 1855) has HR characteristics consistent with trends observed among other reptiles.

Corucia zebrata is a large scincid lizard, endemic to the Solomon Archipelago, where it has been recorded on all major islands (Mccoy, 2006). The monotypic *Corucia* is sister to the remaining genera of the largely Australian *Egernia* group of skinks, comprising *Bellatorias*, *Corucia*, *Cyclodomorphus*, *Egernia*, *Liopholis*, *Lissolepis*, and *Tiliqua* (Gardner *et al.*, 2008a), and last shared a common ancestor with them during the Oligocene (M. Hutchinson, pers. comm.). Two subspecies are recognized, *Corucia zebrata alfredschmidti* from the islands of Bougainville and Buka, and *Corucia zebrata zebrata* found on the remaining eastern islands of the Solomon Archipelago (Kőhler, 1997). The latter subspecies is the focus of our study and hereafter will be referred to as *C. zebrata*. Little is known about the life history, basic ecology or behavior of *C. zebrata* in the wild. Among the many unknown ecological attributes are its HR size, activity levels, movement patterns, and detection probability. Anecdotal observations suggest that *C. zebrata* is nocturnal, arboreal and herbivorous (McCoy, 2006). Indigenous residents of the Solomon Islands report that the lizards inhabit hollows and canopies of strangler figs (*Ficus*). *Corucia zebrata* reaches a snout vent lenght (SVL) of over 300mm and may weigh up to 1,000 g (Kőhler, 1997). This size is comparable to that of the Australian skink *Tiliqua rugosa*, also in the *Egernia* group, which is terrestrial and largely herbivorous and which has a reported HR size of 3–9 ha (Bull & Freake, 1999). In comparison, herbivorous, arboreal iguanian lizards of the same body-size range have smaller HRs of about 1 ha (Perry and Garland, 2000). We provide data on the HR of *C. zebrata* and investigate whether its HR size is similar to those of its scincid relatives or whether it conforms to ecological predictions of a reduced HR compared to more terrestrial species.

We explored three specific aspects of the HR and habitat selection in *C. zebrata*. First, because many other related species in the *Egernia* group show strong site fidelity and long-term HR stability, we expected *C. zebrata* to operate within a defined HR. Second, given that *C. zebrata* is reported to be arboreal and an obligate herbivore, we expected it to have a smaller HR than the more terrestrial *T. rugosa*, in spite of the common ancestry. Finally, we tested, with more detailed observations, local reports that *C. zebrata* has a habitat preference for strangler figs and that it dwells in crevices and holes in the trunks more than in the canopy.

Materials and Methods

Study Area

The study was carried out from 17 April to 24 May 2008, in a 900-ha area of mature, closed canopy rain forest on the island of Ugi (10º14'S; 161º45'E) [datum: WGS84]) in the Solomon Islands. The study area was located approximately 2 km from Suena Village. Rainfall on Ugi is distributed evenly throughout the year, and the island lacks a distinct monsoon season (pers. comm., D. Galvin, Makira weather station, Solomon Islands). The study area contained a high diversity of tree species dominated by the genera *Aglaia*, *Calophyllum*, *Ficus*, *Myristica*, *Pometia*, and *Pterocarpus*. *Ficus* is represented by 63 species in the Solomon Islands (Corner, 1967). Large fruiting strangler figs (*Ficus spp*) were an important forest component in the study area, attracting and often maintaining resident communities of birds, mammals, and reptiles (Corner, 1967). The forest within the study area has been subject to selective logging on a subsistence basis, but the canopy has remained closed, maintaining a sparse understory.

Capture and Measurements

We captured 25 lizards by hand in the daytime, with the help of indigenous people. They climbed up large rain-forest trees, with a mean height of 20–30 m, and emergent trees reaching 40 m, and searched inside hollows and crevices in the trunks and accessible parts of the crowns of the trees, often within the strangler figs infesting them. On the ground, lizards were weighed, and their SVL was measured. Sex was determined by inverting the hemipenes in males. Our sample contained three juveniles (90, 260, and 305 g) and 22 adults (range 375–1,190 g; mean [SE] 685.5 [37.9] g). There were 15 males and 7 females in the adult sample.

Radiotelemetry

A 5.0 g TR-4 radio transmitter (Sirtrack, New Zealand) was attached to the lateral surface at the base of the tail of each lizard using adhesive surgical tape. The mass of the transmitter represented from 0.4–5.5% of the lizard body mass. Lizards were released at the base of the tree from which they had been captured, and they quickly climbed back toward the canopy. Then, we attempted to relocate each lizard, between 0900 and 1700 h each subsequent day, for 5–38 (mean = 25) days, using triangulation from ground level with a TR-4 receiver and a Yagi antennae. Bearing accuracy is compromised when working at ground level with the signal coming from above compared to a two-dimensional environment (Townsend *et al.*, 2007). However, radiotelemetry of arboreal species still allows for significantly improved accuracy in detecting locations compared to visual detection alone (Fedigan *et al.*, 1988). Weather and logistical problems prevented locations on some days. The duration of tracking for each lizard depended on how early in the survey period the lizard was caught and how long the transmitter remained functioning and attached to the lizard. We made a total of 352 location recordings (mean = 14 per lizard; range 3–25).

Defining Home-Range Size

Theory (Schoener, 1981) and empirical studies (Schoener, 1981; Alberts, 1993; Girard *et al.*, 2002) suggest that the estimated HR size should increase with increasing number of records, up to a plateau that represents the true home range. In our study, we characterized the average core area used by the tracked individuals over a short period of time. Hereafter, this area is referred to as the HR area. The HR size was defined as a circular area around the tree where the lizard was first located with a radius equal to the maximum displacement distance. We were not able to quantify the volume of the home range used by individual *C. zebrata*, because of the complex and three dimensional nature of their habitat. Instead, we quantified the two-dimensional footprint area within which the animals moved as has been suggested by Perry and Garland (2000). The trunk of the tree where each lizard was first encountered and released was arbitrarily allocated as the center of its home range. Each new location was then defined by its distance (in meters) from this center. The furthest distance that the lizard was recorded from the center was defined as the HR area radius to calculate HR size. When a lizard was not recorded outside of the central tree, we assumed a HR radius of 5 m around the trunk of the tree. We also determined the proportion of records for each lizard beyond the central tree.

Results

Movements and Site Fidelity

Four lizards were recorded only in the canopy of the central tree of their home range. These lizards all resided in large trees. Two were mature strangler figs, with a trunk diameter at breast height (TDBH) exceeding 3 m. Two were large mature trees (TDBH = 1 m) that were infested with young *Ficus*. The mean maximum displacement distance for all 25 skinks was 19 m (SE = 2.42). No animal moved further than 50 m from its capture site during the tracking period. On average, the lizards were recorded in the capture trees 51% (SE 7.2) of the time.

Home-Range Size

The mean (SE) HR size for *C. zebrata* was found to be 0.16 (0.04) ha. The three juvenile lizards had a mean (SE) HR size of 0.07 (0.034) ha. There was no significant effect of lizard size (regression analysis) or sex (t-test) on HR size. Nor were there any significant correlations between HR size and days tracked or number of fixes acquired.

Habitat

Thirteen lizards were initially found in holes of the trunks of *Ficus*, whereas 12 were found in a range of other tree species. Of those 12, 10 were captured from inside holes and cavities around the tree trunk, whereas two were found in the foliage of broad leaf trees. The high proportion of lizard captures in holes and tree trunk habitats is likely to have been the result of a searching bias by our indigenous assistants. We acquired a total of 226 fixes from the 13 lizards that were found in strangler figs. Our telemetry records showed that 72% of the time (162 fixes), the lizards were located in the *Ficus* tree in which they were first captured, whereas the remainder of the time the lizards were located in the canopies of nearby broadleaf trees. For lizards first captured from trees other than *Ficus*, we acquired a total of 126 location recordings. Of these, the lizards were recorded outside of the capture tree 43% of the time (54) recordings (see Fig. 1). A weighted two-sample Chisquared test indicated that lizards in strangler figs were significantly less likely to leave the tree than were those that were first located in non-*Ficus* trees ($P < 0.001$). In subsequent tracking, lizards found in *Ficus* as well as in other trees were located often in the daytime in low (5–10 m) but dense canopies where they could not be seen. These locations featured a maze of leaves and vines but lacked large branch structures to provide large crevices. Also, the lizards were located frequently in parts of the canopy rich in epiphyte cover. Epiphytes constitute a large and dense cover on most of the trees in which *C. zebrata* is found and large lizards may conceal themselves completely among epiphytes and as such achieve safe refugia on tree structures lacking crevice space. Thus, our radio locations refuted the common perception that these lizards prefer to refuge in crevices around the central trunk of large trees and particularly in strangler figs.

Interactions between Lizards

There were four cases of overlapping HRs of two (two cases) or three (two cases) of the tracked lizards. We found no indication of consistent colocation between the lizards with overlapping HRs. Two cases of overlap were of one and two juveniles, sharing the HR of a larger female. There was no evidence of the juvenile lizards choosing to stay close to the adult or each other within the HRs.

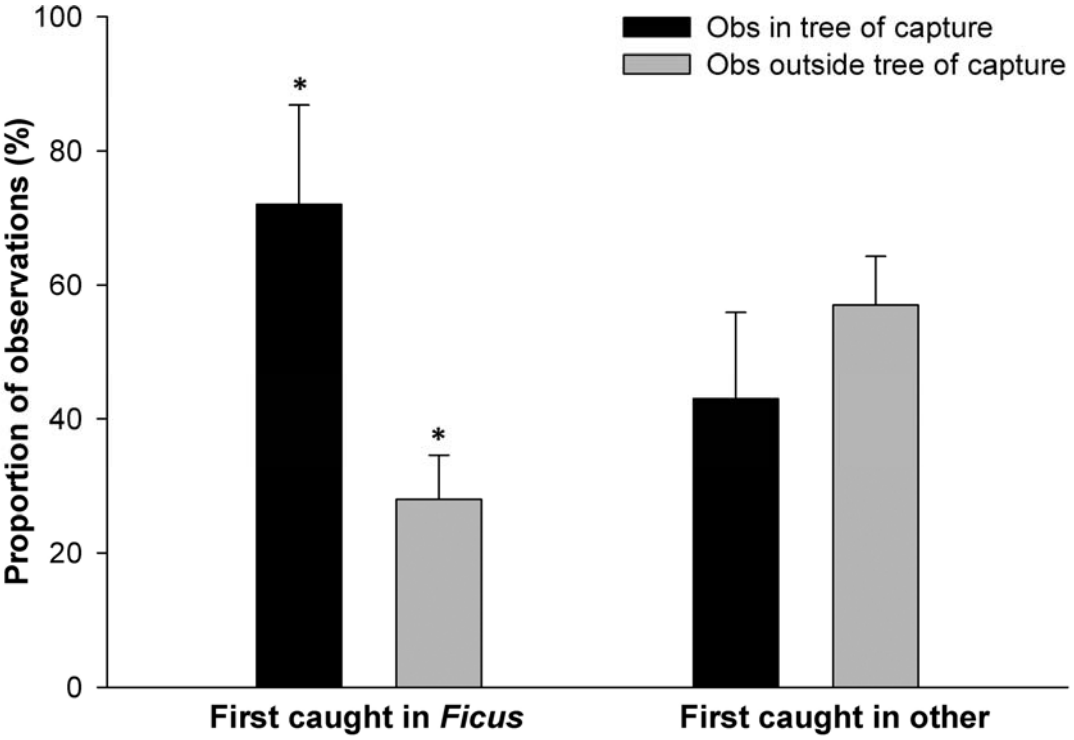

Figure 1: Habitat preference for lizards inhabiting *Ficus* and other trees. Black bars represent the proportion of the observations that the lizards were recorded in the tree of capture. Grey bars represent the proportion of the observations in which the lizards were recorded in trees other than the tree of initial capture. Bars with stars are significantly different from each other. Lizards that were first caught in strangler figs spend more time in the tree of first capture compared with lizards that were first caught in other tree species ($P << 0.01$).

Discussion

Our conclusions are based on a small sample size, particularly of juvenile lizards, that were tracked for a relatively short period of time.

Movements and Site Fidelity

There are a range of challenges associated with telemetry location of arboreal animals using triangulation from below and at a distance of 10–30 m (Townsend *et al.*, 2007). However, we were confident in identifying the tree in which the lizard was located, if not the exact location in the tree. Our data clearly indicated that, within our study period, *C. zebrata* operated within a defined HR area. The observed HR fidelity was consistent with that observed for a wide range of other lizard species, including other species of the *Egernia* group (Bull & Freake, 1999; Duffield & Bull, 2002; Gardner *et al.*, 2002; Kerr & Bull, 2006). Movement to low dense canopy during the day may have been for thermoregulation as reported in captive animals by Mann & Meek (2004).

Home-Range Size

Given the relatively low number of fixes we were able to obtain for individual *C. zebrata*, it is unlikely that we achieved an accurate estimate of the long-term HR size for the species. Over the relatively short period of our study, the mean HR size (0.17 ha) for the animals that we followed was substantially smaller than that of the equivalent-sized and related terrestrial lizard *T. rugosa* (Bull and Freake, 1999; Kerr and Bull, 2006) and of a comparable-sized arboreal primate *Loris tordigradus* (Radhakrishna & Singh, 2002). Unlike the related lizard *T. rugosa* (Bull & Baghurst, 1998), we did not find that HR size increased with body size in *C. zebrata*. This could be because of the relatively poor resolution of our data set and the low number of fixes that were acquired for some of the animals. Furthermore, the crude approach of using the maximum displacement distance as the HR radius may have led to an over-estimation of HR size, and this overestimate may have concealed real differences among lizards of different size or sex. However, logistical issues made it difficult to locate animals at night. *Corucia zebrata* has been reported to be nocturnal; thus, we would expect activity at night. Hence, it is likely that we only captured the daytime refuges in our location records and that the lizards may have moved more extensively during nocturnal foraging. This could have led to us underestimating the size of the HR area used for foraging and the activity level of the lizards.

Habitat

Our data suggest that *C. zebrata* spends most of the time dwelling in the tree canopies rather than in hollows close to the trunk and that they often move to the connected canopies of other nearby trees. From this, we conclude that *C. zebrata* is not restricted to strangler figs, nor does it exclusively require the hollows created by strangler fig trunks. It is likely that the perceived preference of *C. zebrata* for *Ficus* has resulted from the relative ease with which human hunters can climb that tree.

Interactions between Lizards

Although many species in the *Egernia* group show unusually high levels of stable social aggregation (Bull & Baghurst, 1998; Gardner *et al.*, 2001; Chapple & Keogh, 2006), we found no indication of social interactions between *C. zebrata* individuals with overlapping HRs, in the season when we made our observations. In two instances, we found juveniles overlapping in their HRs with a larger female but with no close spatial association.

Detection of Lizards

Because of the logistical difficulties of standardizing the search efforts (only trees accessible to humans could be searched), it is not possible to estimate detection probability using the methods recommended in Mackenzie *et al*. (2002) and Mackenzie & Royle (2005). Given that *C. zebrata* occupies other large rainforest trees at the same rate as they do *Ficus* but can be most readily detected in *Ficus*, one must conclude that the detection probability is heterogeneous depending on the habitat. Additionally, all *C. zebrata* individuals that we followed spent considerable time in the tree canopies, where they have a low detection probability using the conventional survey approach of climbing trees and searching around the trunks. This means that any survey to determine population levels in a particular habitat will be unreliable using current techniques. Camera traps on tree trunks may improve detectability in future studies.

Acknowledgements

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CHAPTER 5:

On the census and effective size of a *Corucia zebrata* population with inferences on the conservation status

A *C. zebrata* on Ugi Island.

Introduction

The number of animals in a population is of paramount interest to ecologists and conservation managers, as smaller populations are at greater extinction risk than are large populations. This is due to Allee effects (inverse density dependance when the population decreases below a given threshold (Allee, 1949)), increased chance of inbreeding with subsequent expression of deleterious alleles (Reed *et al.*, 2003) and increased susceptibility to genetic drift (loss of diversity) and other stochastic events of demographic or environmental nature (Frankham, 2005). Genetic drift will constantly act to reduce genetic variation in a population, whilst mutation and immigration will serve to increase allelic richness. Especially for small populations, genetic drift has been shown to be a much stronger force than mutation and whilst immigration will be a powerful way of introducing new alleles, isolated populations will receive no or few immigrants, thus leaving the allelic richness susceptible to 'erosion' by genetic drift (Lande & Barrowclough, 1987). The likelihood of loosing rare alleles when chromosomes segregate during meiosis will increase with decreasing population size and small populations are at greater risk of loosing rare alleles by chance during catastrophic events that remove individuals from the breeding population (Lande & Barrowclough, 1987). The rate of genetic loss is not merely a factor of the degree of isolation and census population size, but is also affected by sex ratio, mating system and varying reproductive success among individuals. When assessing population size it is therefore important to consider the varying contribution to the gene pool by different individuals. For instance in leking species such as many species of bird of paradise (Pruett-Jones & Pruett-Jones, 1990) and the NZ kakapo (Merton *et al.*, 1984), only a small proportion of males will reproduce (Ryder *et al.*, 2009). For populations displaying such extreme variations in individual reproductive success, the census size is inadequate as an indicator of the rate at which a population loses genetic variation. The rate of genetic loss is determined the effective population size, or N_e, which is a parameter of considerable interest to conservation managers. By definition, N_e refers to the size of a hypothetical, ideal population which is losing heterozygosity at the same rate as the actual population (Wright, 1931). The rate of genetic drift or loss of heterozygosity per generation can be expressed as

$$\frac{1}{2Ne+1} \tag{4.1}$$

where N_e is the ideal population size. Ideal populations are characterized by discrete generations, no migration, constant population size and equal sex ratio, random mating, no mutation or selection and reproductive success being equal for all individuals. These properties are often referred to the Fisher-Wright population model (Fisher, 1930; Wright, 1931). One or more of these hypothetical model properties are generally void in natural populations and for most species the ratio of the effective size to the census size (N_e/N_c ratio) is therefore smaller than 1. Specifically, factors that affect N_e for a population are the mode of reproduction (sexual or asexual), the extent of inbreeding, the mechanism of inheritance (Y-linked loci and autosomal loci have different transmission modes), age structure in the population, bottlenecks in preceding generations and connectivity between populations (Charlesworth, 2009).

Different estimates of N_e will be derived from calculations based on different assumptions. These different calculations result in N_e estimations that are not directly comparable. The most widely used estimates are the inbreeding N_e (N_{eI}) and the variance N_e (N_{eV}). The inbreeding N_e is a measure of decreasing heterozygosity whilst the variance N_e is a measure of changing allele frequencies (Luikart *et al.*, 2010). Additionally, there is the coalescent effective size, which considers all types of genetic change (Luikart *et al.*, 2010) and the eigenvalue N_e which is a measure of the first non-unit eigenvalue of the allele frequency transition matrix (Sjodin *et al.*, 2005). The different methods are applicable to different scenarios; heterozygosity will decrease rapidly during severe bottlenecks whilst allele frequencies will change as a response to inbreeding, which generally occurs after a bottleneck has taken place.

Demographic estimates of N_e

The rate of genetic loss can be estimated from demographic data. The models vary according to the life history and reproductive rates of different species. Engen *et al.* (2007) developed an approach for estimation of N_{eV} for house sparrows (*Passer domesticus*) which is a species with low fecundity. The model incorporates differing reproductive strategies of males and females, the census of each sex, the population size of the rare allele, the number of offspring born to (or sired by) each individual, the variance in number of offspring born to (or sired by) each individual, probability of survival, allele frequency, generation time and growth rate λ. The reproductive success for different individuals was in this case estimated from extensive pedigree data accumulated over several years. Ardren & Kapuscinski (2003) estimated N_{eV} in rainbow trout, which is a species with high fecundity, from the number of breeding pairs per year corrected for unequal sex ratios. Additionally, variance in reproductive success was taken into account, as well as fluctuations in population size and the effective number of breeders in a brood year. These parameters were combined into a comprehensive N_e estimate using the method developed by Lande & Barrowclough (1987) and Waples (2002). Unfortunately, such demographic based N_e estimations can only be used when extensive information on reproductive success and population vital rates is available. This information is generally not attainable for elusive species inhabiting inaccessible habitats, such as *Corucia*.

N_e estimated from genetic data

Over the last decade, several estimators of N_e using genetic data have been proposed (see (Luikart *et al.* 2010) for a review) and are now in frequent use (Beebee, 2009; Boessenkool *et al.*, 2010; Saarinen *et al.*, 2010). Estimations of N_e based on genetic data have previously been considered unreliable due to the frequency of different alleles at neutral marker loci being subject to a high degree of stochasticity at small population sizes (Wang, 2005). These problems remain, but the increasing prevalence of polymorphic markers and improved statistical software has vastly improved genetic N_e estimators (Saarinen *et al.*, 2010). Additionally, estimating N_e from genetic data has the great benefit of being achievable for most wildlife species, as opposed to demographic estimators, which can only be applied to a fraction of populations. The various estimators for N_e using genetic data are based on two fundamentally different sampling approaches; sampling at a single time point and temporal sampling at two different time points when there are different, non-overlapping generations. The latter has until recently been considered the most reliable approach (Saarinen *et al.*, 2010), however single point estimators have the advantage of the samples being more easily acquired and can be applied to long lived species for which sampling across several generations would be difficult. The temporal methods are based on changes in allele frequency between the two sampling points (Wang, 2001) whilst the single point estimators use linkage disequilibrium or heterozygote excess to estimate N_e (Tallmon *et al.*, 2008; Waples & Do, 2008). For a review of N_e estimators, see Luikart *et al.* (2010).

The census size

The census size (N_c) has been defined as the number of adults present in a population or study area (Luikart *et al.*, 2010). The ideal census population size estimate should be a direct count of all individuals in the population (Luikart *et al.*, 2010), an approach that may be challenging even for large conspicuous animals in open habitats. The census size can be estimated using standard population ecology methods such as capture-mark-recapture (CMR) or Bayesian approximation of N_c from the number of recaptures within either a single capture session or two capture sessions. A review of these methods is beyond the scope of this chapter, however, see (Luikart *et al.*, 2010) for a summary of methods. These field methods can be carried out using entirely non-intuitive means such as genetic profiles of animals in population and photo-capture, which operate on the same principals as traditional CMR (Lukacs & Burnham, 2005; Schwartz *et al.*, 2007; Harris *et al.*, 2010).

The N_e/N_c ratio

The ratio between the effective population size and the population census has become an important parameter in conservation ecology. A low N_e/N_c ratio may indicate that a population is subject to demographic contraction as a result of limited genetic diversity even if the number of individuals in the population is relatively high. A N_e/N_c ratio of less than 0.2 has been suggested as a threshold that indicates the population is in danger of extinction (Mace & Lande, 1991). However as stated above, N_e and thus the N_e/N_c ratio are highly dependent on species specific life history traits and the population's genetic history. The N_e/N_c ratios generally vary from 0.2 – 0.5 but may be as low as 0.01 in some species of amphibians and fishes with high fecundity (Frankham, 1995). The N_e/N_c ratio and endangerment of a population should therefore not be assessed without meaningful comparisons to benchmark ratios in other populations of the same or closely related species with similar life histories.

Estimating N_e in a population of C. zebrata

In order for N_e estimates to be meaningful and interpreted correctly, one must be aware of the approach used to estimate N_e as different approaches may yield quite different results (Beebee, 2009; Saarinen *et al.*, 2010). Furthermore, one must be able to make meaningful comparisons to N_e estimates of other populations and related taxa and one must know the parameters that have affected N_e in the taxa of interest. This involves both life history parameters as well as information on the historic range and demography of the species or population. As previously mentioned, the mating system will affect the N_e, as will age structure, population structure and previous bottlenecks. Unfortunately, there is limited research to allow comparisons with N_e of other skink species, and there are many unknown parameters regarding the life history of *C. zebrata*. The mating system of *C. zebrata* is unknown, and the genetic data set presented in this thesis is not large enough to allow for parentage analysis to make inferences on the mating system. The most likely scenarios are random mating and monogamy, both of which are mating systems represented in the *Egernia* group of skinks (Bull, 2000; Chapple, 2003; Stow & Sunnucks, 2004). Populations of *C. zebrata* are age structured with overlapping generations, which is also a factor that would decrease N_e (Charlesworth, 2009). Moreover, founder events of islands result in a bottleneck and subsequent lower genetic variation in the founding population (Grant, 1998). As the population on Ugi Island was probably founded from the nearby Island of Makira, this event is assumed to have reduced the genetic variation in the Ugi population (relative to Makira) and this may affect the estimated genetic N_e. The objectives of the study were 1) to estimate N_e and N_e/N_c ratio for a population of *C. zebrata* on Ugi Island in the Solomon Archipelago and 2) to calculate the rate of genetic drift (e.g. loss of heterozygosity) for the same population in relation to the observed heterozygosity.

Methods

Study site, DNA extraction and PCR amplification

The study site was located on Ugi Island and is described in the Methods section, Chapter 3. The same samples and microsattelite results as described in Chapter 3 were used. Ugi is a small island with a high density of *C. zebrata*. People on Ugi Island are both skilled and motivated to find *C. zebrata*, which greatly facilitated field work on the island.

Census N

It has not been possible to obtain a reliable estimate of the population size of *C. zebrata* on Ugi Island. This is mainly due to the low detection probability of the species (see chapter 4). Additionally, the detection probability is heterogeneous, with individuals in the trunks of strangler figs having a higher probability of being caught, compared to animals in the canopies (of strangler figs and other tree species) which have a probability of being detected that approaches zero. Traditional field ecology methods such as CMR and occupance are extremely challenging when detection probabilities are low and heterogeneous (Lukacs *et al.*, 2007), and the resources to obtain such data did not exist under the conditions of my study. A preliminary estimate of N_c for *C. zebrata* on Ugi Island was based on the basic assumption of a closed population during a sampling session that lasted 6 weeks. Searches for new individuals were made every day, but in new trees within the study area. Animals were found to be largely stationary (Chapter 4), hence it was assumed that movement was negligible. Given that *C. zebrata* is an age structured and long lived species the effect of births and deaths was also considered to be negligible over the six week sampling period. In order to gain an estimate of the N_c on Ugi Island the number of observed adult individuals within the study area was extrapolated by assuming an equal distribution of *C. zebrata* across the entire island. The study area covered approximately 1/5 of the *C. zebrata* habitat on the island. Thus the least number of animals can be calculated to be

$$(\text{observed number of adults})\ 5 \qquad 4.2$$

It is difficult to extrapolate how many individuals existed within the study site, as the detection probability is likely to be very low, hence there will be a considerable number of undetected animals within the study area. An estimate can be made based on recaptures from the radio telemetry study in Chapter 4. At the end of the radio telemetry study, efforts were made to recapture 23 lizards with radio telemetry devices. Five of these were recaptured, hence the detection probability can be estimated to be 0.23 (from 5/23 = 0.23). As the estimate of 0.23 is based on a scenario where the lizards were known to be present in a canopy due to the telemetry device, this number is therefore an overestimate and the realistic detection probability will be lower than this. Here I assume it is somewhere between 0 and 0.23, and have used a range from 0.01- 0.22. The estimated number of animals on Ugi Island is therefore:

$$\frac{\text{(observed number of adults) } 5}{\text{detection probability}} \qquad 4.3$$

Estimation of Ne

The N_{eI} estimator OneSAMP (Tallmon *et al.*, 2008) was used to estimate N_e for *C. zebrata*. This method relies on samples acquired during a single sampling session and is suitable for long lived, age-structured species with overlapping generations. The OneSAMP method is closely related to LDNe though the latter cannot be applied to species with overlapping generations (Waples & Do, 2008). The heterozygote excess (Nb_HetEx) (Zhdanova & Pudovkin, 2008) method requires a bigger sample size than that available for this study and has been found to be unreliable (Luikart *et al.*, 2010). The disequilibrium method by Vitalis & Couvet (2001) assumes knowledge of the mating system, whilst the computer program Colony2 assumes known sibling relationships (Wang, 2009b). OneSAMP was therefore the only N_e estimator applicable to the current data set for *C. zebrata*. Analyses in STRUCTURE and GENELAND (see Chapter 3) strongly suggested that the animals sampled in the current study belong to the same population. All 51 samples were therefore included in the analysis. ONeSAMP is based on Bayesian computation where the prior is a value for N_e defined by the user (Tallmon *et al.*, 2008). The priors must be chosen on a trial basis from a range of possible Ne values. Four different priors for N_e were tested; 60, 250, 500, 1000 and 2000 respectively.

Results

Population census

In total, 37 adults were encountered during the 6 week sampling session. In this period the population was assumed to be closed. Thus, the minimum number of animals assumed to be present on the island can be calculated using formula 4.2:

$$(37)\,5 = 185 \tag{4.4}$$

When correcting for detection probability that is assumed to range from 1-22%, the maximum number of animals on the island can be estimated using formula 4.3 to be:

$$\frac{(37)\,5}{0.01} = 18500 \tag{4.5}$$

Whilst the minimum number of animals present on the island can be estimated to be:

$$\frac{(37)\,5}{0.22} = 841 \tag{4.6}$$

Effective population size

ONeSAMP: For priors up to 1000, ONeSAMP retained moderate and stable N_e estimates ranging from 77 – 132 (mean = 95.5, SE = 12.96). Raising the prior to 2000 resulted in a five-fold increase in estimated N_e to 482 and a wide confidence interval, the latter indicating that the prior is set too far from the actual N_e (Fig. 1). Only results for priors of 60 – 1000 were included in further analysis. It is assumed that the N_e for the study area is representative of the entire island, which – given the high connectivity of the study population (see Chapter 3) is a plausible assumption.

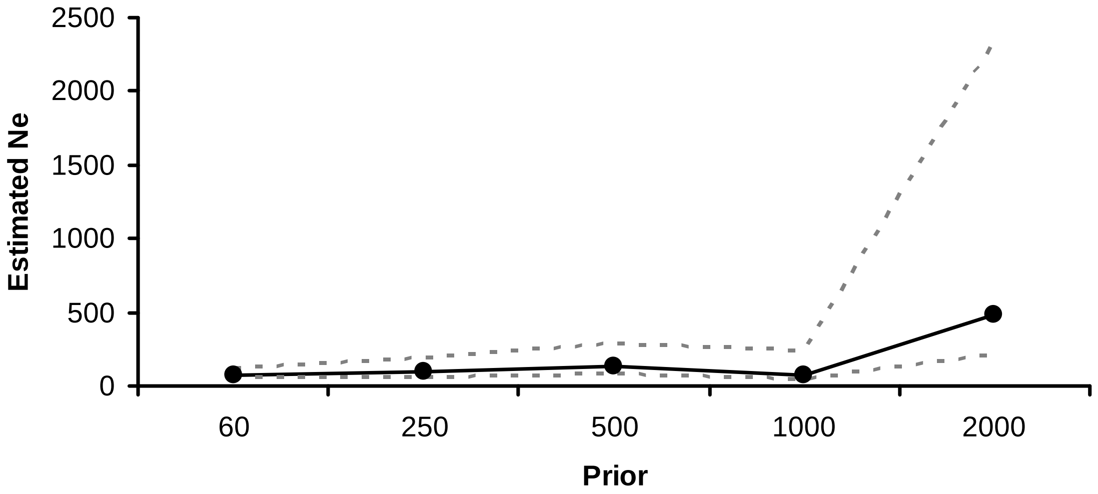

Figure 1: ONeSAMP output with estimated N_e plotted against the priors. Broken lines represent the 95% confidence interval. Black line represents the Estimated N_e for the different priors.

Ne/Nc ratio and rate of genetic drift

When the estimated N_e is substituted in equation 4.1, the loss of heterozygosity per generation on Ugi Island is expressed as:

$$\frac{1}{2(95.5)+1} = 0.0052 \tag{4.7}$$

The N_e/N_c ratio on Ugi Island depends on the N_c. The highest N_c estimate is 18500 and the low extreme of the N_e/N_c ratio range is therefore as follows:

$$\frac{95.5}{18500} = 0.005 \tag{4.8}$$

Similarly, the lowest N_c estimate is 841 and the high extreme of the N_e/N_c ratio range will therefore be:

$$\frac{95.5}{841} = 0.11 \tag{4.9}$$

Thus the range of values for the Ne/Nc ratio is from 0.005 - 0.11. This complete range is below the value of 0.2 that is sometimes considered an indicator of conservation concern.

Discussion

My study provides a measure of the N_e for a population of *C. zebrata* on Ugi Island, in addition to preliminary estimates for a census of the same population, with subsequent N_e/N_c ratio estimations. These results should be interpreted with caution as they are based on the following assumptions: 1) the detection probability for *C. zebrata* is unknown, but has been presented here as a range from 0.01 to the relative high value of 0.22, 2) the accuracy of the N_e estimate for the population has not been tested with other methods, as OneSAMP was the only estimator applicable to the current data set. Because OneSAMP is an inbreeding estimator, it is not ideal for the current data set. As suggested above, inbreeding estimators are most sensitive to loss of genetic variation immediately after a bottle neck, whilst the variance estimators are more sensitive to the inbreeding that occurs following a previous bottleneck. As the population on Ugi is likely to have been through a bottleneck with subsequent loss of genetic variation due to inbreeding, a variance estimator would have been more applicable. However, OneSAMP has been found to be a reliable estimator (as well as the recommended estimator) of N_e, in comparison with a range of other estimators (Beebee, 2009; Saarinen *et al.*, 2010).

The census size for the Ugi population was estimated to range from 841 to 18500, which represents more than a two fold increase from the lowest to the highest estimate. It is plausible that the real value is closer to the upper estimate as *C. zebrata* in all likelihood has a detection probability much lower than 0.22, however more research is needed to accurately determine the detection probability. The detection probability should be estimated separately for different habitat types (i.e. different tree species), as it has been found to be heterogeneous with a higher detection probability in strangler figs (*Ficus*) than on other trees that are less accessible to field workers. Other canopy dwelling species that are detected with spot-lighting have detection probabilities of 0.21 for common ringtail possum and 0.41 for the greater glider (Wintle *et al.*, 2005). A range of detection probability estimates for reptiles were presented in Cunningham *et al.* (2007): the semi-arboreal skink *Egernia striolata* was estimated to have a detection probability of 0.07, that of the large conspicuous lace monitor *Varanus varius* was estimated 0.2, whilst a number of other reptiles were estimated to have a probability of detection that approaches zero. This indicates the large span of detection probabilities for reptiles and it is difficult to use this information to deduce where the detection probability of *C. zebrata* lies in relation to these values.

The estimated N_e/N_c ratio for Ugi Island has a range of 0.005 – 0.11, which is somewhat lower than the values previously reported for age structured species of low fecundity, which generally range from 0.2 – 0.5 (Frankham, 1995) with a median value of 0.14 (Palstra & Ruzzante, 2008). Unfortunately there are no reptilian comparisons for N_e/N_c ratio based on genetic estimators, although four studies of reptiles have used demographic estimations of N_e. One of these is a limited study of eight adult tuatara (*Sphenodon punctatus*) where the N_e/N_c ratio for the population of eight was determined to be 0.47 (Moore *et al.*, 2008a). Given the small sample size it is doubtful whether this can be extrapolated to the tuatara population as a whole. Another is a study of flatback turtle (*Natator depressus*) where no inferences were derived from the calculated N_e/N_c ratio (Theissinger *et al.*, 2009). In the two remaining reptile studies, N_e was estimated for lizards (*Sceloporus olivaceus* and *Uta stansburiana stejnegera*), placing the N_e/N_c ratio at 0.22 and 0.7 respectively (see Frankham (1995) for review). As described above, demographic estimators cannot be directly compared to genetic estimators and the aforementioned ratios are therefore of limited use as comparisons the *C. zebrata* population on Ugi Island. Island populations have lower genetic variation compared to mainland populations (Frankham, 1996), and should therefore be expected to have lower N_e/N_c ratios than mainland populations. Unfortunately there are currently few studies that have focused on the N_e of island populations of low fecundity vertebrate species that allow for meaningful comparisons with the N_e of *C. zebrata*. Boessenkool *et al.* (2010) used a number of different N_{eV} estimators on a population of the threatened yellow eyed penguin (*Megadyptes antipodes*) in New Zealand and found that the N_e/N_c ratio ranged from 0.06 to 0.30, depending on the estimator and the parameters used. More research is therefore required in order to interpret N_e/N_c ratios for island species.

It has been suggested that the rate of genetic drift and the rate of mutation are equal at an effective size of 500, hence that genetic variation in an ideal Fisher-Wright population is stable at this size (Lande & Barrowclough, 1987). Additionally, it has been proposed that in order to maintain inbreeding at less than 1%, an N_e of 50 is required (Franklin, 1980; Simberloff, 1988). This has led to the management recommendation that natural populations should be maintained at effective population sizes of no lower than 50 and preferably 500 to be assumed stable; this rule of thumb has been termed the 50/500 rule (Franklin, 1980; Simberloff, 1988). Provided that the estimated N_e for *C. zebrata* of 95.5 is reliable, there is no immediate concern for the population discussed here. Inbreeding can be considered to be low although the heterzygosity is likely to decrease by a factor of 0.0052 per generation. The current heterozygosity on Ugi has a mean of 0.61 (median = 0.67, SE = 0.08) (Table 1, Chapter 3), thus according to these estimations heterozygosity loss in the Ugi population will have little effect in the foreseeable future.

Given that the *C. zebrata* population on Ugi is on an isolated island, it is possible that the low N_e is partly due to residual low genetic variation as a consequence of a previous founder event and thus that fluctuations in population size will reduce the N_e/N_c ratio (Frankham, 1995).

It is possible to estimate the historical population size for *C. zebrata* on Ugi and detect previous bottlenecks by using Bayesian Skyline Plots for micosatellite data (Heled & Drummond, 2008) in the software BEAST (Drummond & Rambaut, 2007). This analysis combines information from multiple independent loci and estimates the number of population size change points from the data by Bayesian stochastic variable selection (Chipman *et al.*, 2001). A similar analysis of the island from which the lizards on Ugi were derived, Makira, would provide a test for a founder event on Ugi. If the population on Makira has remained constant, it could be implied that the bottleneck on Ugi occurred after the population diverged from Makira. Likewise, it would be interesting to compare the N_e/N_c ratio for Ugi with that of Makira, with the hypothesis that Makira has a higher N_e/N_c ratio than Ugi due to the higher N_e expected for the larger island of Makira. The samples required to carry out this analysis are unfortunately not available.

Conclusions

Given the number of assumptions underlying these results, the N_e/N_c ratio and rate of heterozygosity loss for *C. zebrata* presented in this chapter cannot be considered accurate measures. Rather, a preliminary population census and genetically based N_{eI} estimate for an elusive and iconic species for which nearly no ecological parameters are known has been provided. These estimates suggest no immediate conservation concerns for the *C. zebrata* population on Ugi Island from a genetic perspective, however further research is required in order to obtain a more accurate estimate on detection probability. More studies into the effective population size of island populations would be beneficial to conservation managers who will require meaningful comparisons from which to make informed decisions.

CHAPTER 6

General Summary; Implications for Conservation Management and Avenues of Further Research

A *C. zebrata* being measured in front of a school class on Ugi Island, Makira Prov.

State of the art before the current study

Little was known about *C. zebrata* phylogeography or ecology prior to this study. The available information suggested that *Corucia* constituted two sub-species, but was otherwise evolutionary distinct and had no close relatives in the Solomon Islands and that *Corucia* last shared a common ancestor with its nearest relatives in Australia and New Guinea during the Ologocene, approximately 26 MYA. The sub-species hypothesis had not been verified with molecular methods, and details on the potential sub-species boundary were uncertain. Ecologically, *Corucia* was known to be viviparous, nocturnal, and arboreal with a preference for strangler figs. It was reported to be herbivorous and suspected to be social. The movement pattern of individual lizards was not known, nor was the dispersal pattern, life history traits or population vital rates described. Some populations were thought to have been harvested beyond sustainability, which resulted in a CITES Appendix II listing in 2002 (McCoy, 2006) to limit the export that had depleted many populations, but the conservation status, population densities and effective population sizes on different islands were not known.

In this thesis I have tried to increase our knowledge in as many of the aforementioned topics as possible, although the logistical challenges of working on a nocturnal canopy species in a different cultural and difficult administrative environment, limited the quality and quantity of data that could be acquired during six months in the country, and with the resources that were available. I have elucidated details on the biogeographic history for *C. zebrata*, social behaviour and the genetic structure of a population. The study has included preliminary estimations of a population census and effective population size, more detailed descriptions of habitat preferences, as well as information on movement patterns and home range size. This information will hopefully aid conservation managers in making informed decisions and will facilitate more targeted studies of *C. zebrata* in the future. The different topics are discussed further in the following sections.

State of the art after the current study

Phylogeography

The data presented in Chapter 2 suggest that *Corucia* colonised the Solomon Archipelago within the last 1 - 4 million years. Apart from strong indications that the Western Province was colonised from Choiseul, further details on the colonisation patterns across individual islands are difficult to resolve. As predicted, populations on Choiseul and Isabel were genetically closer together than populations on islands that remained isolated during the Pleistocene glacial cycles, but it was otherwise difficult to distinguish genetic distance as a result of land bridges during the

Last Glacial Maximum from isolation by distance. The fact that samples from most islands were reciprocally monophyletic from the mtDNA analysis suggests that dispersal events have been rare and that populations on each island have resulted from a single dispersal event or source. Though the sampling regime was limited and the number of haplotypes detected probably under-represents what was there, the available data suggest that gene-flow between the islands has been very limited. Furthermore, as populations from the extreme ends of the larger island of Isabel and to some extent Choiseul, were reciprocally monophyletic, dispersal within each island has probably also been limited.

Because samples from Bougainville or Buka were not available, it was not possible to test the sub-species hypothesis put forward in Kőhler (1997). Samples were obtained from the Shortland Islands and analyses based on both mitochondrial (and to a certain degree nuclear DNA) suggest that these are the most divergent samples. This lends support to the suggested hypothesis that the population in the Shortland Islands belong to *C. z. alfredschmidti* (McCoy, 2006), however this can only be verified by incorporating Bougainville samples into the analysis. It is also possible that the animals on the Shortland Islands are the result of a hybridization effect, which again can only be tested using samples from both Bougainville and Choiseul/Isabel. Thus at this stage the status of the two sub species of *C. zebrata* remains unresolved.

Corucia and social behaviour in the Egernia group

There are significant costs associated with group living, including competition for resources and mates (Alexander, 1974), increased exposure to pathogens (Godfrey *et al*., 2006; 2009; Guzinski *et al*., 2009) and a potential risk of increased inbreeding (Pusey & Wolf, 1996). Social traits will therefore only evolve or be maintained when the ecological conditions are such that the benefits outweigh the costs. Known benefits of group behaviour include reduced risk of predation, either through the dilution effect or increased vigilance towards predators in a large group (Elgar, 1989; Lanham & Bull, 2004), or the sharing of limited resources such as refugia with kin (Duffield & Bull, 2002; O'Connor & Shine, 2003).

Many of the highly social *Egernia* group taxa live in environments where they are likely to gain significant benefits from group living. *Egernia stokesii, E cunninghami* and *E. saxatilis* occupy rock outcrops that function as islands scattered across a less hospitable environment. Crevice space on rock outcrops is limited and lizards must share refugia or disperse to other rock outcrops, which again likely are occupied by other individuals which will defend a limited resource (Duffield & Bull, 2002; O'Connor & Shine, 2003; Osterwalder *et al.*, 2004; Chapple & Keogh, 2005). Social groups have been identified also in *Bellatorias major* (Osterwalder *et al.*,

2004) and in *Bellatorias frerei* (Fuller *et al.*, 2005), two species found in sub-tropical woodland habitats, thus indicating that sociality is not entirely habitat dependent and may be an ancestral trait in the *Egernia* group. On the other hand, there are varying degrees of sociality displayed in the various taxa of the *Egernia* group. *Liopholis whitii* and *E. saxatilis* live in groups of 2-6 individuals (O'Connor & Shine, 2003; Chapple & Keogh, 2006), generally a breeding pair and related juvenile, whilst groups of *E. cunninghami* and *E. stokesii* comprise several cohorts of offspring and non-breeding adults of up to 17 individuals that are more related to each other than to lizards in other groups (Gardner, 1999; Gardner *et al.*, 2001; Stow *et al.*, 2001; Gardner *et al.*, 2002; Stow & Sunnucks, 2004). Additionally, different populations of *E. stokesii*, *E. cunninghami* and *E. striolata* display varying degrees of sociality depending on the habitat they inhabit (Chapple, 2003). This implies that there is a degree of plasticity for social traits within these species, and that the degree of social behaviour is partly dependent on the habitat. It is therefore possible that expression of sociality may be aided through ancestry between closely related species and the trait may be a result of both an ancestral condition and recent adaptations to the local environment.

Although we found some genetic evidence for a smaller family structure in *C. zebrata*, that might resemble that of *Bellatorias major*, with a single adult or a pair and several juveniles of several cohorts, the spatial autocorrelation analysis presented in Chapter 3 indicated that one population of *C. zebrata* did not have the above described genetic structure that signifies the large groups of related individuals seen in more highly social species. *Corucia zebrata* is subject to somewhat different selection pressures compared to many of the aforementioned social Australian relatives. It consumes a wide range of leaf matter from trees and epiphytes in addition to flowers and fruit, all of which are readily available in a homogeneous, stable and productive rainforest habitat. Similarly, availability of refugia is unlikely to be a limiting factor as *C. zebrata* dwells in tree hollows of the common strangler fig (*Ficus* spp.) (McCoy, 2006), and amongst epiphytes and foliage of a wide range of trees (Chapter 4), all of which are abundant in the rainforest canopy habitat where *C. zebrata* occurs. Resource limitation is therefore unlikely to play such an important role compared with the rock and grassland living species of the *Egernia* group and is – together with the 26 MYA separating *Corucia* from the rest of the *Egernia* group - highly likely to have affected the social adaptations of *C. zebrata*. Nevertheless, the close association of adults and related juveniles could be evidence that some form of sociality is ancestral to the whole of the *Corucia* - *Egernia* lineage. More research is needed on the behaviour of *C. zebrata*, perhaps in captive colonies, to confirm this.

Genetic structure, N_c and N_e

Results from the small scale genetic structure of a single population showed that the dispersal ability for *C. zebrata* on Ugi is high as no inverse relationship between genetic distance and increasing geographic distance was detected. The population was otherwise unstructured, with all individuals belonging to the same genetic group, which was expected given the homogenous habitat and lack of physical barriers to gene flow. The effective population size (N_e) of the island of Ugi was estimated to 95.5 within the sampling area and given the high inferred dispersal within the sampling area, it is plausible to assume that this number represents the N_e for Ugi Island as a whole. The estimated detection probability, which ranges from 0.01 to 0.22, was used to generate a preliminary census for *C. zebrata* on Ugi Island. As the uncertainty around the census size is large, it follows that the N_e/N_c ratio is also highly uncertain. Although the confidence interval is large (estimated census range from 841-18500), this represents the first attempt to quantify the size and N_e/N_c ratio of a *C. zebrata* population. Only when there are more comparative studies of related taxa will the relevance of this ratio for determining the conservation status of *C. zebrata* become apparent.

Habitat use, home range size and detection probability

As discussed in Chapter 4, radio telemetry of arboreal species is problematic and the accuracy of the method is compromised. Despite this, my telemetry analysis uncovered previously unknown information about *C. zebrata*'s habitat preferences and home range fidelity, albeit for the limited time of up to 6 weeks. *Corucia zebrata* was found to display strong home range fidelity, with a home range that generally constitutes the canopy of one tree, or the canopies of a few closely neighboring trees. The species was reported previously to inhabit mainly strangler figs, whilst my results suggest that *C. zebrata* utilize a wider range of different tree species. Also, it appears that a significant amount of time is spent refuging in the day-time amongst the foliage in tree canopies.

The detection probability was found to be low and heterogeneous; mainly caused by the inaccessibility of canopies to field workers and the difficulty of climbing certain tree species. The detection probability is highest in strangler fig trunks, whilst it approaches nil in large tree canopies. A low and heterogeneous detection probability makes capture-mark-recapture and occupation studies very challenging. Few animals will be captured and these will constitute a very small sampling size. Moreover, only a very small percentage will be recaptured over the period that would constitute a secondary sampling session. For instance, as described in Chapter 4, five out of 23 animals with radio transmitters were recaptured at the end of the telemetry study. Thus, these elusive lizards are difficult to locate and capture even when their presence in a tree is known.

Future directions

My study has contributed significantly to increasing our knowledge about *C. zebrata*, however a number of gaps in the knowledge remain and are described in turn below.

Improved resolution of colonisation pattern and a molecular test of the sub-species hypothesis

A denser sampling scheme across the archipelago would enable a finer resolution of the patterns that have been presented in this thesis. Most importantly, samples from Bougainville or Buka need to be included, in order to test the sub-species hypothesis and determine the initial site of colonisation by *C. zebrata* on the Solomon Archipelago and a better estimate of the age of diversification of *Corucia* in the Solomon Archipelago. Avise & Ball (1990) state that "evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent genetically based traits", hence mitochondrial as well as nuclear loci should be used for this assessment. Efforts should be made to develop more informative nuclear loci than the ones used in this study. Additionally, future analyses would benefit from more samples from Malaita (which should include the two extremes of the island), as well as samples from the southern side of Guadalcanal, and the southern side of Makira, to rule out recent dispersal between adjacent islands that may have not been detected because of the few sample sites and small sample sizes from these larger islands. See Fig. 1 for illustrations on the areas from which samples are currently lacking. Using the extended sampling regime, analysis in the Isolation with Migration (IM) model of population divergence (Hey & Nielsen, 2007) could potentially shed light on the direction of colonisation throughout the archipelago. Additionally, it would be interesting to investigate whether samples from the extreme ends of Makira, Malaita and Guadalcanal adhere to the pattern seen for Isabel and to a certain extent Choiseul, where samples collected from the two extremes of the respective islands are reciprocally monopyletic on mtDNA. Furthermore, the identification of the point at which this reciprocal monophyly for the extreme ends of Choiseul and Isabel (and potentially Makira, Malaita and Guadalcanal) dissolves would shed light on the fine scale biogeographic regions within each island and could be informative in regard to the geographic features that serve as barriers to gene-flow across the islands. As described in Chapter 2, different taxa have different dispersal abilities and the phylogeography of a number of avian taxa on the Solomon Archipelago has been studied (e.g. Filardi & Smith (2005); Pulvers & Colgan (2007)). A complete understanding of the biogeography of the Solomon Archipelago will involve similar studies on taxa with different life history traits and dispersal ability. For instance, amphibians will be more exposed on over-water rafts compared to reptiles and it is possible that arboreal species are more likely to be present on large flotsam compared to terrestrial taxa.

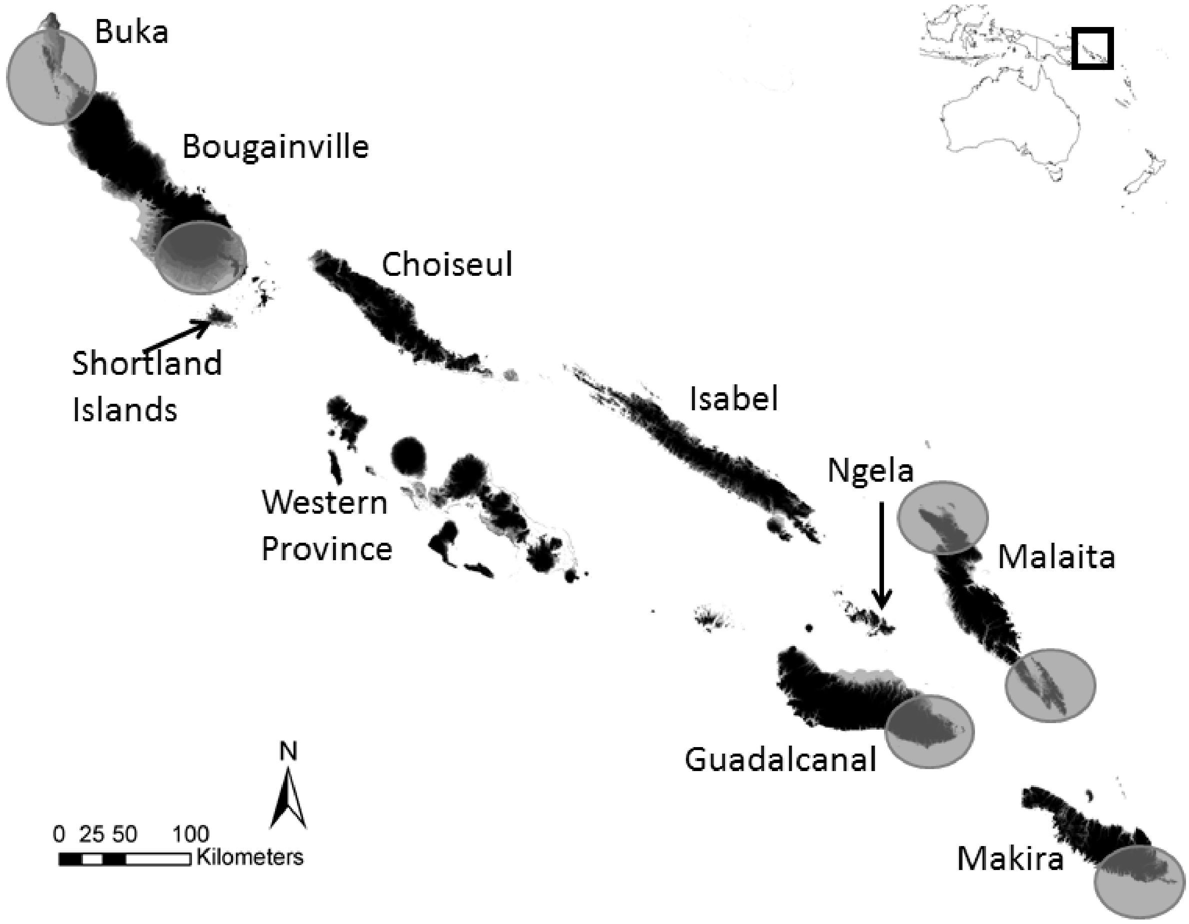

Figure 1: Map of the Solomon Archipelago. Sites where *C. zebrata* should be sampled in order to test the sub-species hypothesis, determine the initial site of colonisation by *C. zebrata* and to improve the estimate of the age of diversification of *Corucia* in the Solomon Archipelago are indicated with gray circles.

Social behaviour

As described in Chapter 3, there were ambiguous results in regard to social behaviour. A larger sample size with more complete sampling of all individuals in a tree and particularly those detected in the same group would increase the power of the analysis. A number of lizards escaped capture (as described in Chapter 3), and this could have skewed my analyses.

Additionally, a potential approach could be the long term and frequent monitoring of easily accessible refuges that are habitually used by *C. zebrata*. This could be done by mounting rope ladders on strangler figs to facilitate accessibility and use of camera traps near refugia. This could shed light on the frequency of use of refuges, and provided animals were caught and individually marked, could yield information on group coherence and composition. This approach is achievable but would be time consuming, and would require a number of field staff. Behavioural studies of wild caught, captive animals could help elucidate the level of interaction between lizards, provided they were presented with a large natural habitat where they could maintain their natural behaviour. It is currently not known how individuals of the species respond to translocation; hence the effect of translocation must be investigated in order to successfully conduct a captive study. An additional challenge will be to provide a captive area large enough for natural behaviour to be maintained, yet still easily monitored at night when the lizards are most active. Direct white light interrupts natural behaviour at night (pers. obs.) and must therefore be avoided.

Population vital rates and abundance

Information on population vital rates is crucial for conservation assessment of species (Mills, 2007). The rates include data on life span and reproductive rates, which can ultimately be used for demographic estimations of effective population size and to calculate the population growth rate, λ (Mills, 2007; Chirakkal & Gerber, 2010). The vital rates are generally established using traditional field ecology methods such as capture-mark-recapture (CMR) (White & Burnham, 1999; Gardner *et al.*, 2010), which is extremely challenging when the detection probability is low and heterogeneous (Lukacs *et al.*, 2007). An extended CMR study will be most easily carried out on Ugi Island, where the species is abundant and local climbers are skilled and reliable. Here, accessible trees within a defined area should be searched repeatedly and thoroughly with given intervals (secondary sampling periods) and over a number of seasons (primary sampling periods). Radio telemetry could facilitate the calculation of the detection probability, which must be estimated separately for different tree species. This approach was not a realistic achievement for the current study, however hopefully the ecological, life history- and capture information presented in this thesis can facilitate a larger and more targeted field ecology study. It is important to note that the vital rates may differ between islands and that vital rates derived from Ugi Island may therefore not be extrapolated directly to other islands.

There is anecdotal information in this thesis that suggests *C. zebrata* in some regions occurs at much lower abundance than on Ugi Island (further information below). The abundance of *C. zebrata* outside of Ugi Island should therefore be investigated, particularly around areas of heavy anthropogenic impact such as Mt Austen (near Honiara) and Ngela Island. Additionally, heavily logged areas should be surveyed as well as the more pristine forest areas in remote areas. Long term CMR effort for abundance surveys would be very difficult to achieve outside of Ugi Island, however an alternative approach could be molecular based N_c estimates. These are based on the principle that animals captured more than once in a session where the population should be considered closed, are regarded as re-captures. Bayesian methods and maximum likelihood can capitalize on the number of occurrences of individual genotypes in a sampling session and estimate N_c for the population. See Luikart *et al.* (2010) for a review of molecular N_c estimators. Genetically based N_e estimations should also be carried out on populations in different regions. Heterogeneity in detection probability due to varying ability amongst people of different regions to locate and capture *C. zebrata* can be overcome by using the same team of climbers at all locations. There will however be additional challenges associated with this approach as traditional owners in many regions will prefer that members of their own ethnic group perform the searches and the chosen climbers may not wish to spend extended time away from their families.

Dispersal and movement pattern

The population genetic data from one population (Chapter 3) strongly suggest that dispersal occurs within homogeneous habitats; however, no such events were detected during the 6 week telemetry study presented in this thesis. It is possible that dispersal may occur at a discrete time of the life history, such as among juveniles or sub-adults (stages not systematically monitored in this study) and that adult animals establish a stable home range after dispersal. A longer radio telemetry study would yield more detailed information on home range size (Schoener, 1981; Alberts, 1993; Girard *et al.*, 2002) and may detect dispersal events. Again, it is recommended that Ugi Island is the site of such studies.

Conservation and management

Conservation status of C. zebrata

Although the conservation status of *C. zebrata* itself is unknown, the habitat in which the species resides is under threat. A scientifically rigorous assessment of the conservation status has proved difficult to conduct, due to the low and heterogeneous detection probability. The low sample size for some areas reflects the difficulty of acquiring samples in the respective regions of the Solomon Islands. On Tetepare Island three to four people searched for 20 days without encountering any *C. zebrata* individuals, even though the species has recently been reported as present on the island (Read & Moseby, 2006). A week was spent on Ngela and produced 1 sample with a number of people searching, whilst 10 samples were acquired from Ugi over a two day period with two people searching. There are large cultural differences in regard to the ability or willingness of local people to catch the lizards; hence the detection probability varies with different regions across the archipelago. It is therefore difficult to separate a potentially low population density from a very low detection probability in the regions where few or no *C. zebrata* were encountered. However it appears that Ugi Island had a higher population density of *C. zebrata* than did other areas that were surveyed and as described in Chapter 5, there appears to be little concern for the Ugi population. However, on places with dense human settlements such as Mt Austen and Ngela (both near the heavily populated capital of Honiara), the *C. zebrata* populations seemed depleted, possible due to a high rate of human consumption and habitat destruction (pers. obs.). Unfortunately, these suspected low population densities can currently not be quantified in a scientifically meaningful manner. Too little information exists for the *C. zebrata* populations on the Shortland Islands, Makira, Maliaita, Choiseul, Isabel and the Western Province to make any inferences on the conservation status of the species in these regions, although habitat destruction is extensive in these areas and may affect the populations (pers. obs.). A complete conservation assessment should quantify the effect of habitat destruction as well as the effect of human consumption on *C. zebrata* population parameters.

Conservation in the Solomon Islands and management recommendations for C. zebrata

Being a fragmented ecosystem, the biota within the Solomon Islands is subject to increased extinction risks, as explained in Frankham (1998). Further fragmentation driven by logging and population expansion occurs on a large scale across the country (Dauvergne, 1998). Only 0.28% of terrestrial ecosystems in the Solomon Islands are formally protected and as a consequence of logging and agriculture, the country ranks within the 10 most threatened forest regions on the planet (Wein & Chatterton, 2005). The Solomon Islands has had an annual population growth rate of 2.3% over the last five years (U.N., 2010a), and has been subject to over a five-fold increase in population since 1950 (W.R.I, 2006). Further significant increases are projected for the future. The need for a conservation effort for the Solomon Islands is therefore apparent. Successful conservation management is based on informed choices in regard to the areas of particular biological importance, the species and ecosystems that will benefit most from conservation management, as well as the prospects and consequences for the local people that rely on natural resources and ecosystem services in the areas of concern.

The definition of Evolutionary Significant Units (ESU) and Management Units (MU) may aid conservation managers in making informed choices in regard to the geographical areas that carry unique genetic variation. The criteria for ESUs and MUs are specific. According to the definition by Moritz (1994), ESUs require 1) adaptive differences between populations, 2) reciprocal monophyly of mtDNA, and 3) significant divergence of allele frequencies at nuclear loci. Adaptive differences have not been investigated; hence recommendations that strictly adhere to the above criteria can not be put forward, although the following inferences can be made from this thesis. In regard to reciprocal monophyly on mtDNA, the criteria are met for all islands (apart from the Westerns Province being nested within Choiseul). Although there are some problems with statistical artifacts in the data set that are likely due to unequal sample sizes, divergence on slowly evolving nuclear loci suggests a degree of structure between the different islands (Chapter 2) and that the Shortland Islands and Makira are particularly different. It is therefore possible that each island constitute separate ESUs, with the exception of the Choiseul / Western Province complex which together constitute an ESU.

For a population to be considered a MU according to the definition presented by Moritz (1994), two of the above criteria must be fulfilled. Alternatively, Palsboll *et al*. (2007) suggests that a population should be considered a MUs if subject to a immigration rate of < 10%. Given the low over-water dispersal ability for *C. zebrata*, every island should by this definition be considered an MU as gene flow per generation between the islands likely approaches zero. Additionally, reciprocal monophyly with respect to the extreme ends of the island of Isabel (as well as high level of differentiation on Choiseul) indicates that populations of *C. zebrata* on a single island may constitute multiple MUs. However, ubiquitous conservation of *C. zebrata* across the archipelago will be difficult to achieve, and a strategy focusing on ESUs that will maximize conservation of genetic variation and evolutionary potential whilst being flexible in regard to the affected regions is suggested. According to McCoy (2006), the Shortland Islands carry the only range of *C. z. alfredschmidti* within the country. Although this sub-species hypothesis has not been tested comprehensively using molecular tools, I have provided data that suggest the lizards sampled from the Shortland Islands are divergent (subject to the small sample size , n=2) on both mitochondrial and slowly evolving nuclear loci (see haplotype networks in Figs. 4 and 5, Chapter 2), and therefore constitute an ESU. The populations on the Shortland Islands should be given a high conservation priority, with efforts to protect populations from over-exploitation and preserve suitable habitat. Additionally, it is appropriate to recommend that efforts are made to conserve *C. zebrata* and viable habitat on each of the larger islands of Makira, Guadalcanal, Malaita, Isabel and on either Choiseul or the Western Province (where Choiseul is recommended as it encapsulates the broad phylogenetic diversity of the Choiseul / Western Province cluster).

Conservation of ESUs and MUs aims to preserve genetic variation for perpetuity, and robustness through climate change (sea level rise; changes in temperature and precipitation) must therefore be factored in. The Melanesian islands of Papua New Guinea and Solomon Islands have been labeled as a wilderness area of significant importance, as they harbour a globally unique ecotype (Cincotta *et al.*, 2000), which is rated amongst the most distinctive ecotypes in the world (Olsen & Dinnerstein, 1998). Similar data for other taxa should therefore be taken into consideration by conservation managers in order to maximize the outcome for the overall biodiversity in the country. These might include native frogs (Menzies, 2006) and the native murids and bats (Flannery, 1995) of the Solomon Archipelago. Additionally, conservation in the socio-economic environment that exists in the Solomon Islands should include opportunity costing exercises involving the local communities that depend on the surrounding ecosystems (Margules & Pressey, 2000). A complete management recommendation for the preservation of the Solomon Island's biota for perpetuity must therefore involve collaboration of researchers or managers working with climate change models, socio-economic models and should consider the biogeography of a number of taxa.

Challenges for conservation management in developing countries

Management recommendations are of limited conservation value unless they can be successfully implemented. Although rich in natural resources, the country of Solomon Islands features on the United Nations list of Least Developed Countries (U.N., 2010b). These countries are characterised by low income, poor standard of education and health care and a weak national economy (U.N., 2010b). Under these socio-economic circumstances conservation implementation can be extremely difficult (Hough, 1988; Kaltenborn *et al.*, 2005; Ormsby & Kaplin, 2005; Ghazanfar, 2008). The rapid population growth puts increasing strain on the Solomon Island ecosystem, however logging by foreign companies remains the biggest threat to biodiversity in the archipelago (Dauvergne, 1998). The negative consequences of logging reach further than direct habitat destruction of the affected area. Logging may cause severe disruption of ecosystem services (Foley *et al.*, 2007), with consequent degrading of fresh water quality (Douglas *et al.*, 1992; Martinez *et al.*, 2009), erosion (Martinez *et al.*, 2009; Blanco-Canqui & Lal, 2010) and detrimental effects on the surrounding coral reefs (Nyström *et al.*, 2000). Ultimately, such degradation of the ecosystem may render the area unsuitable for the traditional subsistence lifestyle based on bush gardening, fishing and hunting, and may force villagers to move into larger cities (Watson, 1996). These negative consequences can be prevented or reduced by measures such as limiting the impact on water ways, restricting harvest to certain species or restoring logged sites, however many local land owners are often unaware of the negative effects of logging due to limited education and may not insist on damage control and restoration prior to signing concession contracts. Additionally, logging companies often do not comply with such agreements and there are few or no sanctions when logging companies abandon their responsibilities (Dauvergne, 1998). Following an assessment of a logging site in the Western Province the National Forest Resources Inventory stated that "the degree of canopy removal and soil disturbance was the most extensive seen by the authors in any logging operation in tropical rainforest in any country" (Dauvergne, 1998).

The process through which logging concessions are granted in the Solomon Islands allows for corruption and is therefore hard to control (Dauvergne, 1998). The Solomon Islands is a signature to the Convention on Biological Diversity (CBD), and is therefore expected to "promote sustainable development" (C.B.D., 2011). However, since signing the convention, logging has occurred at a rate of several-fold the sustainable level (C.B.D., 2010) and the CBD lacks the ability to ensure that signature countries comply with the regulations.

Most of the land in the Solomon Islands (80%) is customary land controlled by local tribes and ultimately the local community controls exploitation of their natural resources (Dauvergne, 1998). Aiding communities in developing alternative and sustainable means to generate revenue will likely slow the rate of unsustainable logging. A measure that would have significant conservation effects is to educate local people about the negative long term effects of unsustainable land use, and how natural resources can be managed sustainably (Ghazanfar, 2008). At the same time local land owners must be presented with, and if necessary aided in development of, alternative means of maintaining their economy. For instance the people of Rendova in the Western Province have developed a cash economy around the Tetepare eco-lodge; an enterprise that currently stops logging companies from entering the largest uninhabited island in the South West Pacific. The Tetepare eco-lodge provides an excellent example of successful conservation management where local people have taken the initiative to preserve the natural forests that they control. This shows that there are alternatives to logging in Melanesian countries and that education and aid to start small sustainable enterprises are at the heart of the issue.

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APPENDIX 1

Table 1: ABTC numbers, date of collection, Island, sample location, latitude and longitude for *C. zebrata* sampled across the Solomon Archipelago and used in Chapter 2. Sample locations refer to letters in Fig.1, Chapter 2. The following samples were used as outgroup samples (ABCT number in brackets): *Egernia depressa* (101643), *E. saxatilis* (6964) and *Lissolepis coventryi* (58241). Some samples were not collected by the author. Collection dates and some GPS locations for these were not available (N/A).

ABTC #	Date collected	Island / Prov.	Location	Latitude	Longitude
112751	17.04.2008	Shortland Isl.	A	-7.11048	155.84810
112752	18.04.2008	Shortland Isl.	A	-7.11048	155.84810
50312	N/A	Choiseul	B	N/A	N/A
50368	N/A	Choiseul	B	N/A	N/A
50412	N/A	Choiseul	B	N/A	N/A
50417	N/A	Choiseul	B	N/A	N/A
50418	N/A	Choiseul	B	N/A	N/A
112753	25.04.2008	Choiseul	C	-7.06440	157.08300
112754	26.04.2008	Choiseul	C	-7.05881	157.09036
112755	26.04.2008	Choiseul	C	-7.05666	157.09364
112756	26.04.2008	Choiseul	C	-7.05310	157.10176
112757	26.04.2008	Choiseul	C	-7.05666	157.09364
112758	26.04.2008	Choiseul	C	-7.05666	157.09364
112759	26.04.2008	Choiseul	C	-7.05881	157.09036
112760	27.04.2008	Choiseul	C	-7.06440	157.08300
112761	27.04.2008	Choiseul	C	-7.05427	157.10970
112762	27.04.2008	Choiseul	C	-7.05415	157.10758
112763	27.04.2008	Choiseul	C	-7.05427	157.10971
92642	N/A	Western Prov.	F	-8.3100	157.5200
92643	N/A	Western Prov.	G	-8.1900	157.4900
98185	10.07.2007	Western Prov.	E	-8.62243	157.33044
98186	10.07.2007	Western Prov.	E	-8.62243	157.33044
98187	10.07.2007	Western Prov.	E	-8.62243	157.33044
98188	12.07.2007	Western Prov.	E	-8.60837	157.32992

ABTC #	Date collected	Island / Prov.	Location	Latitude	Longitude
98189	12.07.2007	Western Prov.	E	-8.61520	157.33188
98190	14.07.2007	Western Prov.	E	-8.61782	157.33061
98191	30.07.2007	Western Prov.	D	-8.31293	157.27008
92645	N/A	Isabel	I	N/A	N/A
92646	N/A	Isabel	I	N/A	N/A
92647	N/A	Isabel	I	N/A	N/A
92648	N/A	Isabel	I	-8.1700	159.3300
92649	N/A	Isabel	I	-8.1700	159.3300
112764	04.04.2008	Isabel	H	-7.59082	158.66660
112765	05.04.2008	Isabel	H	-7.59082	158.66660
112766	05.04.2008	Isabel	H	-7.59082	158.66660
112767	05.04.2008	Isabel	H	-7.59082	158.66660
101358	27.11.2007	Ngela	K	-9.06596	160.29907
92650	N/A	Malaita	J	-9.0700	160.5700
92651	N/A	Malaita	J	-9.0700	160.5700
98192	07.08.2007	Guadalcanal	L	-9.49176	159.98455
98193	09.08.2007	Guadalcanal	L	-9.48809	159.98464
98194	09.08.2007	Guadalcanal	L	-9.48809	159.98464
98195	09.08.2007	Guadalcanal	L	-9.48809	159.98464
101356	14.11.2007	Guadalcanal	L	-9.48625	159.98668
101357	15.11.2007	Guadalcanal	L	-9.48977	159.98959
101341	17.11.2007	Ugi (Makira Prov.)	M	-10.24497	161.75409
101342	18.11.2007	Ugi (Makira Prov.)	M	-10.24316	161.75310
101343	18.11.2007	Ugi (Makira Prov.)	M	-10.24326	161.75260
101344	18.11.2007	Ugi (Makira Prov.)	M	-10.22230	161.73497
101345	18.11.2007	Ugi (Makira Prov.)	M	-10.22230	161.73497
101346	19.11.2007	Ugi (Makira Prov.)	M	-10.23270	161.74234
101347	19.11.2007	Ugi (Makira Prov.)	M	-10.23270	161.74234
101348	19.11.2007	Ugi (Makira Prov.)	M	-10.23270	161.74234
101349	19.11.2007	Ugi (Makira Prov.)	M	-10.24993	161.75721
101350	19.11.2007	Ugi (Makira Prov.)	M	-10.24993	161.75721
101351	24.11.2007	Makira	N	-10.45757	161.94318
101352	24.11.2007	Makira	N	-10.45684	161.94197
101353	27.11.2007	Makira	N	-10.45684	161.94197
101354	27.11.2007	Makira	N	-10.45684	161.94197

ABTC #	Date collected	Island / Prov.	Location	Latitude	Longitude
101355	27.11.2007	Makira	N	-10.45684	161.94197
92652	N/A	Makira	N	-10.3100	161.5500
92653	N/A	Makira	N	-10.3100	161.5500

APPENDIX 2: Uncorrected proof for journal publication

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Home Ranges in the Trees: Radiotelemetry of the Prehensile Tailed Skink, *Corucia zebrata*

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ABSTRACT.—*Corucia zebrata* (Scincidae) is endemic to the Solomon Archipelago and widely distributed across the island group. *Corucia* is evolutionarily distinct and diverged from its nearest relatives about 30 MYA. Little is known about its life history, basic ecology, or behavior in the wild. We conducted a six-week study of movement patterns of *C. zebrata* on the island of Ugi to determine home-range sizes and overlap among conspecifics. Twenty-five lizards were fitted with radio transmitters and were followed for periods of 5–38 days. Telemetry results indicated that the average home range over the period studied was equivalent to the canopy of one tree. Radio-tagged individuals were located more often in the canopy than on the trunk of the tree, where humans typically search for the lizards. The home range is smaller than expected for a similar-sized herbivorous lizard occupying a terrestrial habitat, but the small home range is consistent with results from other arboreal animals. The study increased our knowledge of the behavior and habitat preferences of an ecologically unusual lizard species. We noted that conventional survey methods, searching tree trunk habitats, have low detection probability, an important consideration for further ecological studies of the species, in particular for the purpose of assessing its conservation status.

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Many species retain individual home ranges where they are familiar with the locations of feeding and refuge sites. The home range (HR) of an individual has been defined as the area that contains the requirements for its routine activities such as sheltering, foraging, and reproduction (Burt, 1943). The HR size of a species is often influenced by its foraging and metabolic requirements, and these are usually correlated with body size. Thus, large-bodied species need more food and tend to have larger HRs. This pattern is maintained in both mammals and birds (Harestad and Bunnell, 1979; Lindstedt et al., 1986; Perry and Garland, 2000; Ottaviani et al., 2006). Moreover, because more than 90% of energy is lost between trophic levels, carnivores are expected to need to forage for their energy requirements over larger HRs than equivalent-sized herbivores, a prediction that is supported by many comparative studies (Harestad and Bunnell, 1979; Gittleman and Harvey, 1982; Ottaviani et al., 2006). Specifically, Harvey and Clutton-Brock (1981) reported that, among 20 primate species, those with the most folivorous diets had the smallest HR. Within each trophic level, diet and foraging behavior affect metabolic needs, and these and other ecological factors also can influence HR size. For instance within herbivores, browsers have been found to have larger HRs than equivalent-sized grazers (Mysterud et al., 2001). Additionally, HR size can be influenced by the complexity of the habitat, and Clutton-Brock (1979) showed that arboreal primates that occupy three dimensional habitats have smaller HRs than equivalent-sized primates using more terrestrial and two-dimensional habitats.

The broad patterns of vertebrate HR size variation are maintained in lizards. A comprehensive study by Perry and Garland (2000) comparing 60 species of lizards showed body size to be a strong predictor of HR size and that carnivorous and insectivorous lizards had larger HR sizes than omnivores or herbivores of equivalent size. Perry and Garland (2000) also concluded that lizard species living on the ground had larger HRs than species occupying a three dimensional habitat, such as arboreal lizards occupying tree canopies. We examined whether a little known, arboreal but highly distinctive lizard, *Corucia zebrata* (Gray, 1855) has HR characteristics consistent with trends observed among other reptiles.

Corucia zebrata is a large scincid lizard, endemic to the Solomon Archipelago, where it has been recorded on all major islands (McCoy, 2006). The monotypic *Corucia* is sister to the remaining genera of the largely Australian *Egernia* group of skinks, comprising *Bellatorias*, *Corucia*, *Cyclodomorphus*, *Egernia*, *Liopholis, Lissolepis*, and *Tiliqua* (Gardner et al., 2008), and last shared a common ancestor with them during the Oligocene (M. Hutchinson, pers. comm.). Two subspecies are recognized, *Corucia zebrata alfredschmidti* from the islands of Bougainville and Buka, and *Corucia zebrata zebrata* found on the remaining eastern islands of the Solomon Archipelago (Kőhler, 1997). The latter subspecies is the focus of our study and hereafter will be referred to as *C. zebrata*. Little is known about the life history, basic ecology or behavior of *C. zebrata* in the wild. Among the many unknown ecological attributes are its HR size, activity levels, movement patterns, and detection probability. Anecdotal observations suggest that *C. zebrata* is nocturnal, arboreal and herbivorous (McCoy, 2006). Indigenous residents of the Solomon Islands report that the lizards inhabit hollows and canopies of strangler figs (*Ficus*). *Corucia zebrata* reaches a SVL of over 300 mm and may weigh up to 1,000 g (Kőhler, 1997). This size is comparable to that of the Australian skink *Tiliqua rugosa*, also in the *Egernia* group, which is terrestrial and largely herbivorous and which has a reported HR size of 3–9 ha (Bull and Freake, 1999). In comparison, herbivorous, arboreal iguanian lizards of the same body-size range have smaller HRs of about 1 ha (Perry and Garland, 2000). We provide data on the HR of *C. zebrata* and investigate whether its HR size is similar to those of its scincid relatives or whether it conforms to ecological predictions of a reduced HR compared to more terrestrial species.

We explored three specific aspects of the HR and habitat selection in *C. zebrata*. First, because many other related species in the *Egernia* group show strong site fidelity and long-term HR stability, we expected *C. zebrata* to operate within a defined HR. Second, given that *C. zebrata* is reported to be arboreal and an obligate herbivore, we expected it to have a smaller HR than the more terrestrial *T. rugosa*, in spite of the common ancestry. Finally, we tested, with more detailed observations, local reports that *C. zebrata* has a habitat preference for strangler figs and that it dwells in crevices and holes in the trunks more than in the canopy.

MATERIALS AND METHODS

Study Area.—The study was carried out from 17 April to 24 May 2008, in a 900-ha area of mature, closed canopy rain forest on the island of Ugi (10°14′S; 161°45′E) [datum: WGS84]) in the Solomon Islands. The study area was located approximately 2 km from Suena Village. Rainfall on Ugi is distributed evenly throughout the year, and the island lacks a distinct monsoon season (pers. comm., D. Galvin, Makira weather station, Solomon Islands). The study area contained a high diversity of tree species dominated by the genera *Aglaia*, *Calophyllum*, *Ficus*, *Myristica*, *Pometia*, and *Pterocarpus*. *Ficus* is represented

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by 63 species in the Solomon Islands (Corner, 1967). Large fruiting strangler figs (*Ficus* spp) were an important forest component in the study area, attracting and often maintaining resident communities of birds, mammals, and reptiles (Corner, 1967). The forest within the study area has been subject to selective logging on a subsistence basis, but the canopy has remained closed, maintaining a sparse understory.

Capture and Measurements.—We captured 25 lizards by hand in the daytime, with the help of indigenous people. They climbed up large rain-forest trees, with a mean height of 20–30 m, and emergent trees reaching 40 m, and searched inside hollows and crevices in the trunks and accessible parts of the crowns of the trees, often within the strangler figs infesting them. On the ground, lizards were weighed, and their snout–vent length (SVL) was measured. Sex was determined by inverting the hemipenes in males. Our sample contained three juveniles (90, 260, and 305 g) and 22 adults (range 375–1,190 g; mean [SE] 685.5 [37.9] g). There were 15 males and 7 females in the adult sample.

Radiotelemetry.—A 5.0 g TR-4 radio transmitter (Sirtrack, New Zealand) was attached to the lateral surface at the base of the tail of each lizard using adhesive surgical tape. The mass of the transmitter represented from 0.4–5.5% of the lizard body mass. Lizards were released at the base of the tree from which they had been captured, and they quickly climbed back toward the canopy. Then, we attempted to relocate each lizard, between 0900 and 1700 h each subsequent day, for 5–38 (mean = 25) days, using triangulation from ground level with a TR-4 receiver and a Yagi antennae. Bearing accuracy is compromised when working at ground level with the signal coming from above compared to a two-dimensional environment (Townsend et al., 2007). However, radiotelemetry of arboreal species still allows for significantly improved accuracy in detecting locations compared to visual detection alone (Fedigan et al., 1988). 3 Weather and logistical problems prevented locations on some days. The duration of tracking for each lizard depended on how early in the survey period the lizard was caught and how long the transmitter remained functioning and attached to the lizard. We made a total of 35[illegible] location recordings (mean = 14 per lizard; range 3–25).

Defining Home-Range Size.—Theory (Schoener, 1981) and empirical studies (Schoener, 1981; Alberts, 1993; Girard et al., 2002) suggest that the estimated HR size should increase with increasing number of records, up to a plateau that represents the true home range. In our study, we characterized the average core area used by the tracked individuals over a short period of time. Hereafter, this area is referred to as the HR area. The HR size was defined as a circular area around the tree where the lizard was first located with a radius equal to the maximum displacement distance. We were not able to quantify the volume of the home range used by individual *C. zebrata*, because of the complex and three dimensional nature of their habitat. Instead, we quantified the two-dimensional footprint area within which the animals moved as has been suggested by Perry and Garland (2000). The trunk of the tree where each lizard was first encountered and released was arbitrarily allocated as the center of its home range. Each new location was then defined by its distance (in meters) from this center. The furthest distance that the lizard was recorded from the center was defined as the HR area radius to calculate HR size. When a lizard was not recorded outside of the central tree, we assumed a HR radius of 5 m around the trunk of the tree. We also determined the proportion of records for each lizard beyond the central tree.

RESULTS

Movements and Site Fidelity.—Four lizards were recorded only in the canopy of the central tree of their home range. These lizards all resided in large trees. Two were mature strangler figs, with a trunk diameter at breast height (TDBH) exceeding 3 m. Two were large mature trees (TDBH = 1 m) that were infested with young *Ficus*. The mean maximum displacement distance for all 25 skinks was 19 m (SE = 2.42). No animal moved further than 50 m from its capture site during the tracking period. On average, the lizards were recorded in the capture trees 51% (SE 7.2) of the time.

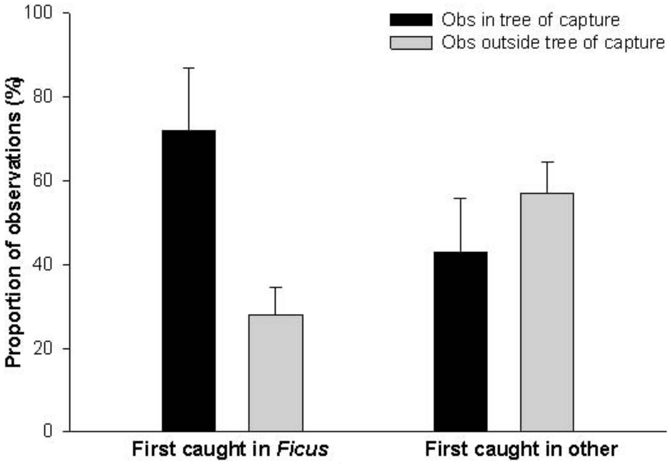

FIG. 1. Habitat preference for lizards inhabiting *Ficus* and other trees. Black bars represent the proportion of the observations that the lizards were recorded in the tree of capture. Grey bars represent the proportion of the observations in which the lizards were recorded in trees other than the tree of initial capture. Bars with stars are significantly different from each other. Lizards that were first caught in strangler figs spend more time in the tree of first capture compared with lizards that were first caught in other tree species ($P << 0.01$). 4

Home-Range Size.—The mean (SE) HR size for *C. zebrata* was found to be 0.16 (0.04) ha. The three juvenile lizards had a mean (SE) HR size of 0.07 (0.034) ha. There was no significant effect of lizard size (regression analysis) or sex (*t*-test) on HR size. Nor were there any significant correlations between HR size and days tracked or number of fixes acquired.

Habitat.—Thirteen lizards were initially found in holes of the trunks of *Ficus*, whereas 12 were found in a range of other tree species. Of those 12, 10 were captured from inside holes and cavities around the tree trunk, whereas two were found in the foliage of broad leaf trees. The high proportion of lizard captures in holes and tree trunk habitats is likely to have been the result of a searching bias by our indigenous assistants. We acquired a total of 226 fixes from the 13 lizards that were found in strangler figs. Our telemetry records showed that 72% of the time (162 fixes), the lizards were located in the *Ficus* tree in which they were first captured, whereas the remainder of the time the lizards were located in the canopies of nearby broadleaf trees. For lizards first captured from trees other than *Ficus*, we acquired a total of 126 location recordings. Of these, the lizards were recorded outside of the capture tree 43% of the time (54) recordings (see Fig. 1). A weighted two-sample Chi-squared test indicated that lizards in strangler figs were significantly less likely to leave the tree than were those that were first located in non-*Ficus* trees ($P < 0.001$). In subsequent tracking, lizards found in *Ficus* as well as in other trees were located often in the daytime in low (5–10 m) but dense canopies where they could not be seen. These locations featured a maze of leaves and vines but lacked large branch structures to provide large crevices. Also, the lizards were located frequently in parts of the canopy rich in epiphyte cover. Epiphytes constitute a large and dense cover on most of the trees in which *C. zebrata* is found and large lizards may conceal themselves completely among epiphytes and as such achieve safe refugia

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on tree structures lacking crevice space. Thus, our radio locations refuted the common perception that these lizards prefer to refuge in crevices around the central trunk of large trees and particularly in strangler figs.

Interactions between Lizards.—There were four cases of overlapping HRs of two (two cases) or three (two cases) of the tracked lizards. We found no indication of consistent colocation between the lizards with overlapping HRs. Two cases of overlap were of one and two juveniles, sharing the HR of a larger female. There was no evidence of the juvenile lizards choosing to stay close to the adult or each other within the HRs.

Discussion

Our conclusions are based on a small sample size, particularly of juvenile lizards, that were tracked for a relatively short period of time.

Movements and Site Fidelity.—There are a range of challenges associated with telemetry location of arboreal animals using triangulation from below and at a distance of 10–30 m (Townsend et al., 2007). However, we were confident in identifying the tree in which the lizard was located, if not the exact location in the tree. Our data clearly indicated that, within our study period, *C. zebrata* operated within a defined HR area. The observed HR fidelity was consistent with that observed for a wide range of other lizard species, including other species of the *Egernia* group (Bull and Freake, 1999; Duffield and Bull, 2002; Gardner et al., 2002; Kerr and Bull, 2006). Movement to low dense canopy during the day may have been for thermoregulation as reported in captive animals by Mann and Meek (2004).

Home-Range Size.—Given the relatively low number of fixes we were able to obtain for individual *C. zebrata*, it is unlikely that we achieved an accurate estimate of the long-term HR size for the species. Over the relatively short period of our study, the mean HR size (0.17 ha) for the animals that we followed was substantially smaller than that of the equivalent-sized and related terrestrial lizard *T. rugosa* (Bull and Freake, 1999; Kerr and Bull, 2006) and of a comparable-sized arboreal primate *Loris tordigradus* (Radhakrishna and Singh, 2002). Unlike the related lizard *T. rugosa* (Bull and Baghurst, 1998), we did not find that HR size increased with body size in *C. zebrata*. This could be because of the relatively poor resolution of our data set and the low number of fixes that were acquired for some of the animals. Furthermore, the crude approach of using the maximum displacement distance as the HR radius may have led to an over-estimation of HR size, and this overestimate may have concealed real differences among lizards of different size or sex. However, logistical issues made it difficult to locate animals at night. *Corucia zebrata* has been reported to be nocturnal; thus, we would expect activity at night. Hence, it is likely that we only captured the daytime refuges in our location records and that the lizards may have moved more extensively during nocturnal foraging. This could have led to us underestimating the size of the HR area used for foraging and the activity level of the lizards.

Habitat.—Our data suggest that *C. zebrata* spends most of the time dwelling in the tree canopies rather than in hollows close to the trunk and that they often move to the connected canopies of other nearby trees. From this, we conclude that *C. zebrata* is not restricted to strangler figs, nor does it exclusively require the hollows created by strangler fig trunks. It is likely that the perceived preference of *C. zebrata* for *Ficus* has resulted from the relative ease with which human hunters can climb that tree.

Interactions between Lizards.—Although many species in the *Egernia* group show unusually high levels of stable social aggregation (Bull and Baghurst, 1998; Gardner et al., 2001; Chapple and Keogh, 2006), we found no indication of social interactions between *C. zebrata* individuals with overlapping HRs, in the season when we made our observations. In two instances, we found juveniles overlapping in their HRs with a larger female but with no close spatial association.

Detection of Lizards.—Because of the logistical difficulties of standardizing the search efforts (only trees accessible to humans could be searched), it is not possible to estimate detection probability using the methods recommended in MacKenzie et al. (2002) and Mackenzie and Royle (2005). Given that *C. zebrata* occupies other large rain-forest trees at the same rate as they do *Ficus* but can be most readily detected in *Ficus*, one must conclude that the detection probability is heterogeneous depending on the habitat. Additionally, all *C. zebrata* individuals that we followed spent considerable time in the tree canopies, where they have a low detection probability using the conventional survey approach of climbing trees and searching around the trunks. This means that any survey to determine population levels in a particular habitat will be unreliable using current techniques. Camera traps on tree trunks may improve detectability in future studies.

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