DEMOGRAPHY AND CONSERVATION OF THE FLOREANA RACER (*Pseudalsophis biserialis biserialis*) ON GARDNER-BY-FLOREANA AND CHAMPION ISLETS, GALÁPAGOS ISLANDS, ECUADOR

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ABSTRACT

The Floreana Racer (*Pseudalsophis biserialis biserialis*) is a medium-sized colubrid endemic to the islets of Gardner-by-Floreana and Champion off the coast of Floreana Island, in the South of the Galápagos Archipelago. The subspecies was historically abundant on Floreana Island, as indicated by sub-fossil remains, however is has since been extinct there since the late 1800's as a result of the effects of large-scale habitat modification, fires and the introduction of rats and cats. I conducted the first field study on the population size, inter-island morphological variability and the diet of the Floreana racer on the two islets where the species occurs as a first step towards the translocation of Floreana racers to Floreana Island. Fieldwork took place over 30 days between November 2015 and January 2017. With the assistance of eight colleagues and volunteers I conducted daylight searches for Floreana racers yielding a total of 123 individuals, 20 on Champion and 103 on Gardner-by-Floreana. Of these 119 individuals were marked with unique PIT-Tags. I also conducted a mark-recapture estimate of population size on both islets based on 17 recaptures. The resulting estimate of the global population of the subspecies is approximately 3088 individuals (Champion 209 snakes; Gardner-by-Floreana: 2879 snakes). I also investigated the diet of Floreana racers via analysis of faecal samples from 29 individuals. The most common prey items are lava lizards (*Microllophus grayii*), followed by the Floreana gecko (*Phyllodactyllus baueri*). Lastly I discuss the conservation status of the subspecies and future areas of research and management to advance the knowledge, and conservation status of the Floreana Racer.

RESUMEN

La culebra de Floreana (*Pseudalsophis biserialis biserialis*) es una colúbrido de mediano tamaño endémica a los islotes de Gardner-por-Floreana y Champion, cerca de la costa de Isla Floreana, en el sur del Archipiélago de las Galápagos. Esta subespecie era abundante históricamente en la Isla Floreana, como lo indican restos sub-fósiles. Sin embargo, se extinguió en Isla Floreana a finales de los 1800's como resultado del efecto combinado de modificaciones de hábitat a nivel de paisaje, fuegos, y la introducción de ratas y gatos. Lleve a cabo el primer estudio de campo sobre el estado poblacional, variabilidad morfológica entre islotes y la dieta de la culebra de Floreana en los islotes mencionados, como un primer paso hacia la reintroducción de la especie a la Isla Floreana. La colecta de datos se llevo a cabo durante 30 días en campo entre Noviembre 2015 y Enero 2017. Con la asistencia de ocho colegas y voluntarios, lleve a cabo búsquedas de culebras durante las horas del día, que resultaron en la captura de 123 individuos (20 en Champion y 103 en Gardner-por-Floreana). De éstos, 119 individuos fueron marcados mediante la implantación de "PIT-Tags". Lleve a cabo una estimación poblacional basada en marcaje-recaptura en ambos islotes en base a 17 recapturas. El estimado poblacional global es de 3088 individuos (Champion: 209; Gardner-por-Floreana: 2879). También investigue la dieta de la culebra de Floreana. Las presas mas comunes fueron las lagartijas de lava (*Microllophus grayii*) y el gecko de Floreana (*Phyllodactylus baueri*). Finalmente, presento una discusión sobre el estado de conservación de esta subespecie y áreas para investigación futura.

DECLARATION

The research presented is part of a larger research project on Galápagos Terrestrial Snakes developed since 2015 by my supervisor Dr. Luis Ortiz-Catedral. Dr. Ortiz-Catedral allowed me to execute this project following approved protocols by the Ministry of Environment, Ecuador via the Directorate of the Galápagos National Park. Dr. Ortiz-Catedral coordinated all the logistical support necessary to complete this investigation, and also obtained the relevant permissions for accessing study sites. Dr. Ortiz-Catedral and I jointly prepared funding applications to cover the costs incurred during this investigation. Said funds were obtained from the Mohamed bin Zayed Species Conservation Fund, Auckland Zoo Conservation Fund, Rufford Small Grants Program and Galápagos Conservation Trust. The ideas about the components of this thesis were discussed between my supervisor and I prior, during and after fieldtrips. Dr. Ortiz-Catedral provided all the supervision necessary for the development of this project, the analysis of results and the elaboration of the final document. I assume all responsibility for mistakes or omissions present in this document.

Eli J. Christian

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CHAPTER 1

GENERAL INTRODUCTION

A Floreana racer (*Pseudalsophis biserialis biserialis*) on Champion Islet, off the Coast of Floreana Island.

Photo: Jenny Daltry.

1.1 ABSTRACT

Snakes represent a diverse, widespread group of ectothermal vertebrates, which remains understudied in the wild, despite their important ecological role as predators, their common association with humans, and the popularity of several species as pets. This scarcity of studies, for such a large and diverse group, makes it difficult to assess the conservation status of snakes globally, because such assessments rely on available information about species, their habitats and ecological requirements. This situation also constraints the development of specific management programs aimed at improving the conservation status of threatened species. The available body of research on snakes has largely concentrated on species from temperate habitats in Europe and North America. Except for studies on a few tropical Australian species, there is a remarkable paucity of studies on tropical snakes, particularly those inhabiting Central and South America. In general, continental species have been studied more than island species. The research presented here focuses on a rare tropical species endemic to the Galápagos Islands, Ecuador: the Floreana racer. Over two field seasons I conducted the first demographic study on this micro-endemic species, and obtained information to better understand its morphological variability. This study aims to lay the foundation for a management plan for the species that will improve its conservation status in the near future by reintroducing the Floreana racer to its historical range.

1.2 INTRODUCTION

1.2.1 Diversity and Conservation Status of Snakes (Squamata: Serpentes)

The order Serpentes (Squamata: Reptilia), which includes all the reptiles known as “snakes” is a group of ectothermic amniotic vertebrates characterized by having an elongated body, scales, forked tongues, specialized scent organs as well as a lack of external limbs and eyelids (Mattison, 2007). Snakes are a diverse group of approximately 3000 species grouped into 18 families (Fry, 2005; Weins et al., 2012). These families are distributed worldwide, but with higher diversity in and around the tropics, and a marked decrease in species numbers towards the Poles (Conant & Collins, 1998; Gaston, 2000). Snakes can be found on every continental landmass, except Antarctica and on the majority of smaller landmasses as well, with the exceptions of Ireland, Iceland, Greenland, New Zealand, the Hawaiian Archipelago and a number of smaller islands in the Pacific and Atlantic oceans (Conant & Collins, 1998). Despite their diversity and wide distribution, snakes remain a poorly studied order of vertebrates. Snakes are cryptic, or occur at low densities, making even basic ecological studies challenging.

Despite their uniform body plan, snakes are highly diverse in their morphological, physiological and behavioural adaptations. These adaptations allow them to inhabit a wide array of niches despite the constraints imposed by the ectothermic life. Their range of body sizes and weights best exemplifies the morphological variability among snakes. The size of individual snakes can vary greatly between species, sexes and even within species (Boback, 2003; Madsen & Shine, 1993; Richard Shine, 1978). The largest species, regarded as “giant snakes” (Richard Shine, Harlow, Keogh, & Boeadi, 1998b) are all constrictors (family *Boidae*) and occur in tropical or subtropical locations (Reed & Rodda, 2009). The Burmese python (*Python bivittatus*) is considered to be one of the largest species of snake, with an individual known as “Baby” reaching 5.74 m in length at the time of its death (Barker, Barten, DVM, Ehrsam, & Daddono, 2012). In contrast, the smallest snake species, the Barbados threadsnake (*Tetracheilostoma carlae*), has been documented reaching lengths of 100 mm in adult specimens and weighing under 1 gram (Hedges, 2008).

There is also considerable variability in sexual size dimorphism in most snakes (Madsen & Shine, 1994). Several hypotheses have been proposed to explain the occurrence of extreme sexual dimorphism (Camilleri & Shine, 1990). Male biased dimorphism occurs most commonly in species that exhibit intraspecific sexual competition for mates (Richard Shine, 1978, 1994). Female biased dimorphism occurs most frequently in species where there is an apparent relationship between the size of an individual and the number of young it can produce (Madsen & Shine, 1994). Male or female biased size dimorphism can differ within species and across geographic localities (Pearson, Shine, & Williams, 2002).

Patterns of sexual size dimorphism extend also to the head widths of individuals. Head width dictates the size of prey an individual snake can ingest, suggesting a niche diversification causality as opposed to a sexual selection driver (Richard Shine, 1991). Niche diversification as one of the driving mechanisms of sexual size dimorphism among snakes also provides an explanation for the observed diversity of body sizes (Kozłowski, 1989). Larger head and body sizes allow for the ingestion of larger prey. Larger species of snake, such as the reticulated python (*Python reticulatus*), commonly have female-biased sexual size dimorphism, with males reaching a maximum size of 5 m while females can grow to 7 m (Richard Shine, Harlow, Keogh, & Boeadi, 1998a).

1.2.2 Physiology and behaviour

Snakes also differ greatly in physiological performance (Castoe et al., 2013). The evolutionary history of snakes highlights the extensive physiological adaptations (Hsiang et al., 2015), including the loss of limbs, the functional loss of one lung and the elongation of body and internal organs (Vidal & Hedges, 2004). The most diverse physiological adaptation among snakes is the production of venom in specialized organs for the subjugation of prey (Chippaux, Williams, & White, 1991). Venom is a toxic compound injected into prey or to cause rapid death or incapacitation (Fry et al., 2012). Venoms are a highly diverse physiological feature of snakes, with every species having an identifiable venom (Juárez, Comas, González-Candelas, & Calvete, 2008).

There are four main ways venom affects cells and each species has a unique venom formed by a combination of polypeptides and proteins (Boldrini-França et al., 2017; Matsui, Fujimura, & Titani, 2000): anticoagulant, coagulant, cytotoxic and neurotoxic venom. These types of venom can affect organisms in different ways. Anticoagulant, coagulant and cytotoxic venoms modify tissues which results in the death or incapacitation of prey (Kini, 2005; Kourie & Shorthouse, 2000). Neurotoxic venoms affect systems such as the neural system or the cardiovascular system to incapacitate or kill prey (Kini, 2003; Yamazaki et al., 2002). These venoms have evolved across the superfamily Colubroidea (Vidal, 2002) commonly referred to as “advanced snakes”. These venoms have evolved via the repurposing of normal physiological proteins (Fry et al., 2006; Fry & Wüster, 2004).

The behaviour of snakes is also highly variable. Many species are reclusive and inhabit areas with little human habitation. For example, the Papuan black snake (*Pseudechis papuanus*) found on the island of Sabai, is highly reclusive to the point that very little was known about the species despite co-existing with humans since their settlement on the island (Konar & Modak, 2010; Parkin & Allen, 2013; Roodt, De Titto, Dolbab, & Chippaux, 2013). Behaviorally some of these species avoid human interaction by hiding or moving when they detect, through smell or vibration, human presence (Konar & Modak, 2010). Other species interact with humans through their residence in human settlements, like cities or towns (Chippaux, 1998). The species that reside alongside humans, often come into conflict with residents when they enter human dwellings by accident or in search of prey (Brock & Howard, 1962).

A study conducted in the Monduli district, in Northern Tanzania, found that 97% of the respondents from the study villages had encountered a snake at least once and 74% had encountered snakes more than three times (Nonga & Haruna, 2015). Taxonomic classification of the interacting species, revealed 12 species residing within the study villages, six of which were venomous species. Species such as, the Black Mamba (*Dendroas pispolylepis*), Boom slang snake (*Dispholidus typus*), black necked spitting cobra (*Naja naja nigricollis*), Egyptian cobra (*Naja haje*), red spiting cobra (*Naja pallida*) and the puff adder (*Pseduaspis cana*) are all venomous snakes that were found within the confines of both study villages (Nonga & Haruna, 2015). Other species are less disturbed by the presence of humans, which leads to conflict (Nonga & Haruna, 2015). In general, most humans are afraid of snakes, dangerous or not, which accentuates the presence of a snake in a domestic dwelling (Stanley, 2008).

Snakes have most frequently been observed whilst interacting with humans. However there are other snake behaviours that are noteworthy and highly diverse, particularly mating behaviours (D. Duvall, Schuett, & Arnold, 1993). (Brattstrom, 1974). Species in the temperate zones, such as the red-sided garter snake (*Thamnophis sirtalis parietalis*), predominantly spend winter in burrows and emerge in the early spring, when mating occurs (Brattstrom, 1974; Richard Shine & Mason, 2001). This is known as assemblage mating and only occurs once a year (D. Duvall et al., 1993).

Snakes in lower latitudes, such as the prairie rattlesnake (*Crotalus viridis viridis*), distributed from Canada to Mexico, engage in mate-searching behaviour (David Duvall & Schuett, 1997). This involves males of the species actively searching for receptive females, sometimes over great distances (Brown & Weatherhead, 1999). The distribution of females is the most crucial factor, with males often failing to find a suitable mate (Brown & Weatherhead, 1999; David Duvall & Schuett, 1997). In a study conducted by Duvall and Schuett (1997) on the prairie rattlesnake (*Crotalus viridis viridis*), 57% of the males failed to find a female over the course of the mating season. Once males find a receptive female there is often multiple males competing for the right to mate with her leading to intra-sexual competition for access (R. Shine et al., 2000).

Being ectotherms snakes also possess a number of behavioural adaptations specific to maintaining adequate body temperatures for physiological processes. To sustain cellular metabolism there is a minimal threshold of external heat input required. Snakes are able to influence the rate at which they absorb heat through behaviour, such as basking or seeking shade (Sunday, Bates, & Dulvy, 2011; Sunday et al., 2014). The body temperature of ectotherms is the most important factor that affects their fitness, all aspects of their biology depend on it (Angilletta et al., 2002). Despite the behavioural thermoregulatory factors of most ectotherms, environments with extreme lows in temperature and thermal input do not provide minimal levels for metabolism. Environments with constant highs in temperature and thermal input can also be detrimental to ectothermic organisms. Exposure to extreme temperatures above the thermal sensitivity of macromolecular structures can result in the dissociation of these molecules, resulting in their inactivity and irreparable cellular damage or the death of the organism (Hoffman, Chown, & Clusella-Trullas, 2013).

The restriction of environmental factors translates into a restriction in the available habitats that can be successfully occupied by ectotherms

(Darlington, 1948). Ectotherms possess varied thermoregulatory behaviours that are dependent on the species and environment in question. Within ectotherms there are two behavioural methods to adjust to external temperatures: Thermoconforming species rely on matching their body temperature to local conditions through passive action. Thermoregulating species regulate body temperature to an optimal value, either through physical orientation (e.g. moving to areas of higher temperature) or through metabolic processes (Herczeg, Kovács, Hettyey, & Merilä, 2003). The majority of ectothermic species use a combination of both methods to achieve sufficient thermal energy for metabolism, or to maintain body temperatures under thermal maximum (Seebacher & Shine, 2004). The use of one or both of these methods is still heavily reliant on the environmental conditions and local conditions, such as predation risk and foraging opportunities (Blouin-Demers & Weatherhead, 2002). This reliance on environmental factors limits the distribution of ectotherms, in particularly larger species (Seebacher, Grigg, & Beard, 1999).

Ectotherms have an optimal temperature where physiological processes are most efficient; at temperatures higher or lower than the optimal the organism has suboptimal level of physiological processes. This is known as a 'thermal performance curve' (Huey & Stevenson, 1979). Thermal performance curves highlight both the optimal temperature and the critical temperatures. If an ectotherms core body temperature gets too high above or too far below optimal it can cause irreparable cellular damage and even death (Lutterschmidt & Hutchison, 1997). The thermal maximums and minimums of individual ectotherm species are theorized to have evolved in response to the local environmental conditions (Angilletta et al., 2002). For example, the Sidewinder (*Crotalus cerastes*), a desert dwelling snake, has a thermal maximum, determined in laboratory conditions, of 41.8°C (Cowles & Bogert, 1944). In contrast, the common ribbon snake (*Thamnophis sauritus*), which inhabits northeastern America as far north as Canada, has a much lower thermal maximum, of only 32.7°C (Rosen, 1991).

The most important factors for determining the suitability of habitats for reptiles are the average temperature and the percentage of shade cover (Kearney, Shine, & Porter, 2009). Equatorial latitudes, due to their high average temperatures and high percentage of shade cover, house the greatest number and diversity of reptile species. The density of reptiles steadily decreases as latitude increases or decreases, with the Polar Regions possessing no reptile species (Darlington, 1948; Richard Shine & Madsen, 1996; Vitt, 1987).

1.3 GLOBAL CONSERVATION STATUS

Although snakes are widespread in terrestrial and aquatic ecosystems their conservation status has received less attention than other taxonomic groups, such as mammals or birds (Clark & May, 2002; Germano & Bishop, 2008; Mittermeier & Carr, 1992; Pandey, Khadka, & Papes, 2015). This taxonomic bias makes it difficult to generate a clear picture of the global conservation status of snakes. There are some species and localities that have been studied extensively, but there is a much higher proportion of species and localities that lack study (Tolley, Alexander, Branch, Bowles, & Maritz, 2016). Many species in Africa, South America, Asia and Australia still lack satisfactory study (Böhm et al., 2013). Despite the varying level of study, several threats to ectotherms in particular have been identified. One threat that will impact ectotherms in particular, is global climate change (Deutsch et al., 2008). As previously stated all ectotherms have an optimal temperature, which has evolved in tandem with the local environmental conditions. Global climate change threatens this relationship by altering the average temperature to levels that could be detrimental to ectothermic organism (Clusella-Trullas, Blackburn, & Chown, 2011; Huey & Kingsolver, 1993). This is predicted to be the most severe in tropical ecosystems where the average temperatures are currently high, and many ectotherms are close to their thermal maximum (Deutsch et al., 2008).

Another significant threat to snakes is the legal and illegal animal trade of wild specimens. Snakes are taken for pets, food, traditional medicines, and skins (Nijman, 2010). This affects snake populations from all regions, but it is particularly prevalent in highly prized or desirable species, for example, 5337 green pythons (*Morelia viridis*) are collected from Indonesia each year. Or the Broad headed snake (*Hoplocephalus bungaroides*) from Australia, in 1997 85% of females from the population in Morton national park were removed by collectors (Lyons & Natusch, 2011; Webb, Brook, & Shine, 2002).

The trade of snakes is not restricted to a specific geographic region, with records of illegal trade of species recorded for snake populations in Italy (Filippi & Luiselli, 2000), the United States (Stallins & Kelley, 2013; Sullivan,

2000) and Peru (Daut, Brightsmith, & Peterson, 2015). China has high levels of removal of animals from wild populations for captive breeding (Zhou & Jiang, 2004).

The exotic pet trade is also prevalent in the United Kingdom. In 2005 the trade in reptiles alone was estimated to be £200 million (Robinson, St. John, Griffiths, & Roberts, 2015). Many of the traded animals are bred in farms for the express purpose of being sold. The most damaging impact occurs when animals are taken from the wild to be sold. This results in a loss of animals from the wild, thus altering the ecosystem, these animals are then sold to private owners many of whom are unable to adequately care for these animals (Robinson et al., 2015). Additionally before the animals even reach the consumer, many die as a result of transport or mistreatment by the dealers (Ashley et al., 2014; Bush, Baker, & MacDonald, 2014).

An investigation by Ashley et al. (2014) into an exotic animal wholesaler revealed that 80% of the 26,400 exotic animals were injured, sick or dead. Animals bred in captivity and packed in large numbers for transport suffer extremely high mortality rates, a conservative estimate made by Redford in 1992 that three animals die for every live one that is traded (Redford, 1992). The pet trade, both legal and illegal is causing a significant impact on reptile populations worldwide. While this is not a threat that affects all species snakes, it has significant impacts on a number of species.

The identification of species-specific threats requires detailed studies to highlight local factors. These factors are often shared by neighboring species, thus highlighting threats at the landscape or ecosystem level (Akçakaya, 2001). These informative studies are important for the effective management of ecosystems, as they can identify previously unidentified threats and/or highlight conservation issues (Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998).

Snake populations have been studied most widely in the continental United States, Australia, the British Isles, a number of locations in Europe and South-eastern and central Asia (Todd, Wilson, & Gibbons, 2010). However, not all of the documented snake species have complete IUCN assessments (The International Union for Conservation of Nature). This situation promoted the Global Reptile assessment (GRA) that aims to provide thorough conservation assessments for reptiles globally. By 2013 the GRA had completed comprehensive assessments of the all the reptile species in North America, Madagascar and New Caledonia, also assessments of the endemic species of Europe, Philippines and a number of smaller island groups were completed. This highlighted the geographic taxonomic bias, with Latin America, Africa, parts of Asia and Australia only progressing slowly in this time (Böhm et al., 2013) (see Chapter 5 for more detail). Latin America has a high level of snake endemism due to a number of unique habitats, such as the Amazon rainforest. Rainforests harbour high numbers of species diversity; this combined with the size of the Amazon rainforest indicates a large number of endemic species (Mayer & Pimm, 1997; Novotný et al., 2006; Soares-Filho et al., 2006). However, due to the complex and hazardous nature of the rainforest, it is difficult to perform accurate ecological studies (Novotný & Basset, 2000). The difficulties of rainforest studies combined with the difficulties of studying snakes results in a lack of information on the majority of rainforest snakes.

1.4 SNAKES ON ISLANDS

Islands provide an ideal environment to study snakes (Bonnet, Pearson, Ladyman, Lourdais, & Bradshaw, 2002). Islands serve as an excellent opportunity for ecological studies, due to their high diversity of unique species and their isolated geography (Emerson, 2002). Island ecosystems are generally simpler than mainland ecosystems. This is due to their constrained geographical features, and also because in general island populations have a reduced input of new individuals (Bonnet et al., 2002). Island populations of snakes face limited resources within a well defined space (surrounded by water), limited habitat availability and limited potential mates (Gillespie & Baldwin, 2009).

An island population will have a different set of biotic and abiotic factors than a mainland population of the same species. All energetic input into an ecosystem is limited by the primary trophic level, due to a snake's predatory behaviour they are reliant on the primary and secondary consumers below them to fix the energy into a form that they can access (Barnes, Maxwell, Reuman, & Jennings, 2010; Benoit-Bird, 2004). This process is restricted due to the isolated nature of island ecosystems. A mainland ecosystem can receive new energetic input in the form of prey items moving through the ecosystem from fringe areas and other neighbouring populations, island populations do not have this input based solely on their locality (Hanski, 1998).

Island-endemic species, particularly on small islands, are at a much greater risk of extinction than mainland species (Frankham, 1997; Manne, Brooks, & Pimm, 1999). A recent survey of historical and avian extinctions and their causes from the year 1500 onwards determined that species' extinctions on islands represented 95% of the recorded mammalian and avian extinctions. Avian extinctions on islands were 187 times higher on islands than on continental land masses, and 177 times higher for mammals (Loehle & Eschenbach, 2011). Thus, understanding the dynamics of island populations of snakes can provide a valuable insight into the processes of contemporary extinction.

The cause of this susceptibility is still unclear; there are a number of potential biotic and abiotic factors, (Frankham, 1998). Genetic factors, such as genetic bottlenecks, and the founder effect, can affect small populations. Essentially, any loss of genetic variability on small isolated populations reduces the material upon which natural selection can occur (Frankham, 1998). Thus, understanding the changes in the genetic constitution of island population of snakes has the potential to illustrate the effects of conservation management on the viability of species and populations (Lande, 1998).

Islands are particularly susceptible to catastrophic environmental factors. For example, a study on the effects of Hurricane “Lili” on the biota of a number of islands in the Bahamas; found that smaller species are affected more drastically than larger species (Spiller, Losos, & Schoener, 1998). The same study noted that there was no relationship between population size and survivorship for catastrophic disturbances (Spiller et al., 1998). It is due to catastrophic environmental factors, e.g. hurricanes that a number of authors have suggested that most island populations go extinct before genetic impacts can affect them (Caughley, 1994; Lande, 1988; Pimm, Jones, & Diamond, 1988).

However, a more recent study has called this theory into question by analyzing the levels of heterozygosity of small populations (Spielman, Brook, & Frankham, 2004). The authors found that 77% of threatened taxa had a lower hereozygosity than related non-threatened taxa. This is indicative that both genetic and environmental factors are impacting small populations on islands.

The formation of an island archipelago is an important component when considering the nature of colonization. Ocean archipelagos can be classified, based on their origin, into two groups. The islands in the archipelago are either remnants of land that were previously attached to the continental landmasses and have since eroded away or been separated due to changes in the sea level, or they are the result of volcanism. Volcanic islands arise through volcanic action on the sea bed and eventually form islands above sea level (Santamarta, Lario-Bascones, Rodríguez-Martín, Hernández-Gutiérrez, & Poncela, 2014). In contrast, islands with a continental origin were previously part of continental landmasses, and have been present above sea level since their breakaway (Kreft, Jetz, Mutke, Kier, & Barthlott, 2008).

The nature of island formation is indicative of potential colonization patterns. One method posited to explain the dispersal of species to continental islands is across so called land bridges. These land bridges form based on the sea level at the time and can connect continental landmasses with what are now islands. Land bridges allowed for terrestrial organisms to reach localities which are now separated from their ancestral habitat, thus providing an over land dispersal mechanism (Foufopoulos & Ives, 1999).

A number of vertebrate taxa are unsuited for dispersal over open water. Therefore colonization of offshore islands is considered rare. Ectothermic species rely on temperature to metabolize (Harlow, Hillman, & Hoffman, 1976). Temperature transference through water occurs at higher rates than through air, due to the thermal conductivity of the medium (Kreith & Black, 1980). A study on the wandering garter snake (*Thamnophis elegans*) found that when predating on aquatic species at sub-optimal temperatures, the cellular process were occurring at 36% of optimal rate (Stevenson, Peterson, & Tsuji, 1985). Despite the difficulties for reptilian species to disperse over water to islands, there are a number of instances where it has occurred.

Although instances of island colonization by terrestrial snake species exist, there are further issues these species face after colonization. An additional issue these species face is the their ability to disperse between neighbouring islands or populations. Colonization of island by reptiles is a rare occurrence, indicating there must be other factors to consider. A study in 2011 of an oceanic archipelago off the south east coast of Japan provided a valuable insight into the possible dispersal of a snake species. The authors discovered that snake populations on five islands were all derived from a single colonization event, whereas, another island in the same archipelago has been colonized at three separate instances, highlighting the random patterns of reptilian colonization events on islands (Kuriyama et al., 2011). However, despite the unique nature of reptilian colonization of islands, very little study has been undertaken into these species, and as such they remain largely undocumented.

1.5 DEMOGRAPHIC STUDIES ON ISLAND SNAKES

Demographic studies are important for providing the basic information of a species. Such as fecundity, mortality, rates of immigration and emigration, sex ratios, population size, and territorial distribution (Scheidel, 2009; Xie, 2000). Due to the basal information they provide, demographic studies are important for developing conservation and management plans for a species (Lande, 1988; Vucetich & Waite, 2003). Demographic studies are most beneficial when undertaken on previously unstudied species, due to the basal information that they provide. This information can be directly used to conserve the species.

Demographic studies on snakes have focused on the study of sex ratios, ecosystem constraints, genetic diversity, rates of immigration and emigration, thermoregulatory behaviours as well as mortality and fecundity (D. Duvall et al., 1993; Lelièvre et al., 2013; Osypka & Arnold, 2000; Prior, Gibbs, & Weatherhead, 1996). Demographic studies support the effective conservation management of a species owing to the basic biological information they provide (DeSalle & Amato, 2004). For this purpose, those studies that have been undertaken on snakes are of critical importance.

Populations can be quantified by defining the number of individuals of a given species that occupy a discrete area (Gaines, Harrod, & Lehmkuhl, 1999). The discrete nature of a defined population allows for effective, and accurate modeling of biological factors, such as fecundity, mortality, immigration and emigration (Barros, Bassanezi, & Tonelli, 2000). This is particularly relevant for island populations. Islands provide a finite available habitat for any given animal population thus enabling the analysis of discrete areas used by members of the population (Emerson, 2002). The finite nature of the habitat, limited immigration and emigration and constant environmental factors, across the geographic range, reduces the errors associated with modeling populations (L. Thomas, Buckland, Newman, & Harwood, 2005).

Islands have a different set of limiting factors and colonization patterns compared to mainland ecosystems (see Chapter 3 for more detail). Frankham (1996) discussed how the genetic diversity of island populations tends to be lower than mainland counterparts. Preserving a significant portion of the genetic diversity of threatened species is a common goal of management plans; thus determining the population size on islands of species of conservation interest is central to devise plans that could conserve the most genetic diversity.

Several studies of island species have also been undertaken on snakes. Tiger snakes (*Notechis scutatus*) on Carnac Island in Western Australia, Grass snakes (*Natrix natrix*) on Gotland in Sweden and Barbados threadsnakes (genus *Leptotyphlops*) in the Lesser Antilles (Bonnet et al., 2002; Hedges, 2008; Luiselli, Filippi, & Capula, 2005). The Antiguan racer (*Alsophis antiguae*) also known as the ‘rarest snake in the world’, has received intensive management on the islands that it inhabits (Jenny C. Daltry et al., 2001). It has also been translocated to neighboring islands within the same archipelago (Jennifer C. Daltry, 2006). Although a number of snake species have been studied on islands, there are still a number of species and localities with very little study. One such locality with a number of endemic snake species that has received very little investigation is the Galápagos Archipelago.

The Galápagos Archipelago is a chain of volcanic oceanic islands, situated 906 kilometers off the west coast of South America (Caccone, Ketmaier, & Powell, 1999). From the first settlement of humans in early 20th century the human population has continued to grow, in the late 1980’s the population was 15000 residents (Bremmer & Perez, 2002). The Galápagos is a province of Ecuador and is managed through the Ecuadorian government, and has a local department in charge of management and monitoring, the Directorate of the Galápagos National Park (hereafter GNP). This is the organisation responsible for the management of the Islands’ natural resources and the protection of the endemic species. The Galápagos Islands hold a prestigious place amongst scientists for the role they played in shaping Darwin’s theory of Evolution by Natural Selection (Freeman, 1985). They also have a high number of endemic species and unique lineages, which has ultimately lead to the classification of the Galápagos islands as one of the 25 hot spots of global biodiversity (Myers et al., 2000).

The identification of the Galápagos as a hotspot of biodiversity and its influence on the theory of evolution has translated into a high degree of scientific investigation. There are a number of Non-governmental organizations (NGOs) who solely fund research in the Galápagos, as well as NGOs who have permanent facilities on the Islands, such as the Charles Darwin Research Station (Taylor, Hardner, & Stewart, 2008). This high degree of scientific input has resulted in a thorough investigation of a number of the ‘charismatic’ species of the Islands.

Darwin’s finches, so named due to the impact they had on Darwin’s Theory of Evolution by Natural Selection, are grouped into five separate genera: *Geospiza* contains six species, *Camarhynchus* contains five species, *Certhidea* contains two and the genus of *Pinaroloxias* and *Platyspiza* both contain one species (Burns, Hackett, & Klein, 2002). Darwin’s finches are one of the most extensively studies in the archipelago, first studied by Darwin during his 1835 voyage to the Islands (Darwin, 1891). Since then, several studies have investigated their diets, distributions, genetic diversity, breeding and reproductive patterns (Burns et al., 2002; Grant & Grant, 2002; León, Podos, Gardezi, Herrel, & Hendry, 2014), making Darwin’s finches the most extensively studied species in the archipelago.

Another iconic group of species that have received extensive study and management are the Galápagos Giant tortoises (*Geochelone* spp.). Galápagos giant tortoises have been monitored in the wild, and managed through captive breeding since the mid 1960s (Milinkovitvh et al., 2004). The Galápagos Giant land iguana (*Conolophus subcristatus*) is also monitored and has been translocated, with a number of individuals kept in captivity (Gibbs, Snell, & Causton, 1999; Tzika et al., 2008). Marine iguanas (*Amblyrhynchus*) have also been studied in particular regarding the physiological adaptations that allow them to sustain a partial marine existence as ectotherms (Wikelski, 2005; Wikelski & Romero, 2003). Although numerous studies have focused on Galápagos reptiles, there are a few reptile groups that have received little attention.

The Galápagos is home to seven species of Lava Lizard (*Microlophus* spp.), six endemic species of Gecko (*Phyllodactylus* spp.) as well as six species of endemic snakes (*Pseudalsophis* spp.) (R. A. Thomas, 1997; Torres-Carvajal, Barnes, Pozo-Andrade, Tapia, & Nicholls, 2014). Very little is known about the evolutionary history of these smaller reptiles and studies to date have been mostly descriptive, focusing on their patterns of distribution, and general biology. The phylogenetic history of endemic geckos and lava lizards has been studied (Kizirian, Trager, Donnelly, & Wright, 2004), but there has not been a parallel development addressing the diversity of Galápagos snakes.

The snakes of the Galápagos Islands (Zaher et al., 2009) represent 86% of the diversity of *Pseudalsophis,* making this genus a predominantly island group. The only continental species described to date is *Pseudalsophis elegans*, which inhabits mainland Ecuador, Chile and Peru (Richman & Böhm, 2011). The remaining six species of the *Pseudalsophis* genus inhabit the

Galápagos Islands. These six species were grouped into *Pseudalsophis* in 2009 on the basis of their hemipenial morphology (Zaher et al., 2009). The species were previously classified in the genus of *Alsophis* or *Antilophis* based on the work of a number of authors (Günther, 1860; R. A. Thomas, 1997)(see Chapter 2 for more detail). Very little information about these species is known. There have been a number of specimens collected from various expeditions to the Galápagos, since Darwin (Heller, 1903; Van Denburgh, 1912).

The current distribution and diversity of the genus of *Pseudalsophis* in Galápagos, is based on the work of Robert Thomas (Figure 1.1). Thomas examined museum specimens of snakes collected in the Galápagos and, based on scale counts and morphological features, refined the taxonomy and distributions (R. A. Thomas, 1997). In contrast to the numerous studies addressing the taxonomy of *Pseudalsophis,* there has only been one study focusing on the biology of these reptiles.

Altamirano (1996) studied the relationship between activity levels and thermal physiology of *Pseudalsophis hoodensis* and its prey on the Española Island (Altamirano, 1996). This study determined that snakes on Española exhibit a bimodal pattern of activity, and that the distribution of snakes on the study site can be partially attributed to the distribution of their common prey, the Española lava lizard (*Microlophus delanonis*).

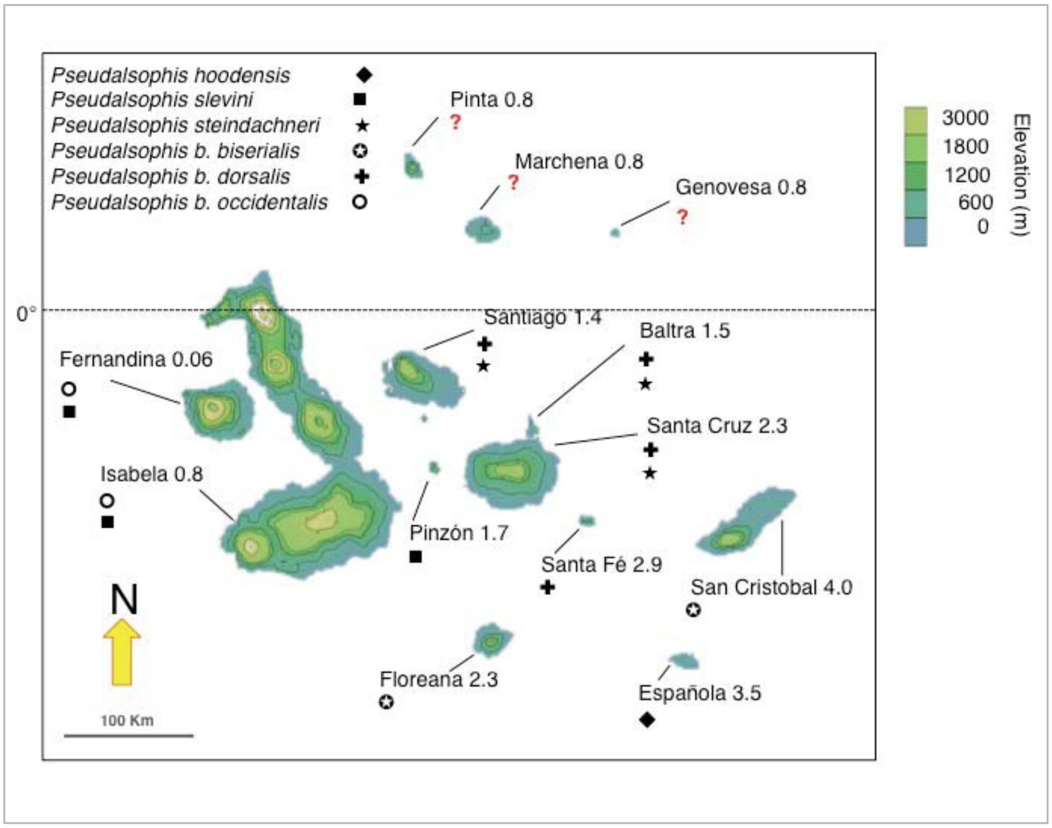

Figure 1. Map of the Galápagos Islands showing the distribution of six *Pseudalsophis* taxa. Numbers next to the Island's name represent age in my.

1.6 THE PRESENT STUDY

In the previous sections of this Chapter, I have discussed how, compared to other vertebrate taxa, the biology and conservation status of snakes remains poorly studied. Further, I have highlighted the potential of island populations as ideal systems to study the biology of snakes. My study focuses on the rarest of the Galápagos snakes, the “Galápagos racer” also known locally as Floreana racer (*Pseudalsophis biserialis biserialis*). For the remainder of this thesis the local name will be used. The Floreana racer is currently restricted to two islets off the coast of Floreana Island in the south of the Galápagos archipelago, adding to 90 hectares of available habitat. A second subspecies, the San Cristobal racer (*Pseudalsophis biserialis eibli*) occurs on San Cristobal Island and neighboring islets (Mertens 1960) predonminantly on lowland scrub.

Preliminary observations indicate that the San Cristobal and Floreana racers might indeed be separate species due to their different arrangements in scale series, hemi-penes morphology and colouration (Ortiz-Catedral pers. comm.). For the remaining of this thesis, both taxa will be considered subspecies.

The Floreana racer is considered locally extinct on Floreana Island. Searches for this sub-species on Floreana Island were conducted in 1905-1906 and 2012, without success (Fritts & Fritts, 1982; Steadman, 1986; Van Denburgh, 1912). Floreana Island has a long history of ecological degradation, chiefly due to the introduction of mammals associated with the progressive human settlement of the island from 1832-1930. During this period at least seven species of vertebrates, including the Floreana racer, have become locally extinct (Steadman, 1986).

Since 1999, the GNP conducts large-scale eradications and control of introduced mammals, including goats, donkeys, pigs and more recently rats and cats on various islands, including Floreana (Carrion, Donlan, Campbell, Lavoire, & Cruz, 2007; Island Conservation, 2013). Following the removal of these introduced species, the ecological restoration plans for Floreana consider the reintroduction of locally extinct species like the Floreana mockingbird (*Mimus trifasciatus*) (Hoeck et al., 2010) and the Floreana racer (Island Conservation, 2013) in the near future. While the biology of the Floreana mockingbird has been studied recently (Deem, Parker, Cruz, Merkel, & Hoeck, 2011; Ortiz-Catedral, 2014), facilitating the development of a management plan (Ortiz-Catedral, 2013), no parallel effort has taken place for the Floreana racer.

My thesis thus represents the first scientific contribution to understanding of the biology of the rarest and most range-restricted sub-species of *Pseudalsophis* as a first step towards the development of a management plan for this sub-species, for the reintroduction of *Pseudalsophis biserialis biserialis* to its historical range on Floreana island. My thesis presents for the first time, information on the morphological variability of this species on Champion and Gardner-by-Floreana islets, the first observations on its diet and the first estimation of population size on both these islets. Additionally, my thesis identifies priority areas for future research.

1.6.1 Study species

My research is focused on the Floreana racer, one of the two subspecies of *Pseudalsophis biserialis* (*sensu* Mertens, 1960): *P. biserialis biserialis* from Floreana Island, and Champion and Gardner-by-Floreana islets (Figure 1.2); and the San Cristobal racer (*P. biserialis eibli*) from San Cristobal Island and islets (Mertens, 1960). The Floreana racer was first described in 1860 by Günther based on the only live specimen ever collected on Floreana Island, by Charles Darwin in 1835 (Günther, 1860). A full description of the Floreana racer is presented in Chapter 2.

1.6.2 Study sites

I conducted this research on Champion and Gardner-by-Floreana Islets. Champion Islet (Figure 1.3a) is located 600 meters off the northeastern coast of Floreana Island. It has as total size of 9 hectares and maximum elevation of 46 metres above sea level (Grant, Curry, & Grant, 2000). Gardner-by-Floreana islet (Figure 1.3b) has a total size of 81 hectares, due to inaccessibility to most of the islet, I concentrated on a 17 hectare plateau on the eastern side of the islet.

The habitat on both islets consists of lowlands vegetation characterized by patches of *Opuntia megasperma*, *Cordia lutea*, *Parkinsonia aculeata*, *Croton scouleri*, *Scalesia affinis* and *Jasminocereus thouarsii* (only on Champion Islet). Both islands retain large areas dominated by exposed lava rock.

Figure 1.2. A Floreana racer (*Pseudalsophis biserialis biserialis*) (arrow) in its habitat on Gardner-by-Floreana. Floreana Island (8 km away) in the background. Photo: L. Ortiz-Catedral.

Figure 1.3. Examples of lowlands vegetation on Champion (above) and Gardner (below) islets. Note the *Opuntia*-*Croton scouleri* association in the foreground. Photo: L. Ortiz-Catedral.

1.7 THESIS AIMS AND OBJECTIVES

My research has the overall aim of providing information on the morphological variability, population size, diet and overall conservation status of the Floreana racer, to help develop a strategy for the reintroduction of the species to its historical range.

Objective 1. Present an updated description of the Floreana racer based on observations from live individuals in the field.

I obtained morphological measurements of individuals in the wild in the only two known populations of Floreana racer: Champion and Gardner-by-Floreana islets. I provide the first analysis of morphological variation, scale symmetry and weight ranges in the wild for a Galápagos terrestrial snake. This information is presented in Chapter 2.

Objective 2. - Estimate the population size and size classes of the Floreana racer on Champion and Gardner-by-Floreana islets.

I determined the population sizes of the Floreana racer *Psedualsophis biseralis* on the islets of Champion and Gardner-by-Floreana. To achieve this goal, I inserted handled individuals with a unique micro-transponder for the purposes of individual identification upon the event of recapture. I then used the numbers of capture and recaptured individuals in a mark-recapture model to determine the average population numbers for each islet. This information will become useful under the context of a translocation plan for the purpose of reintroduction. This information is presented in Chapter 3.

Objective 3. Describe the diet of the Floreana racer.

I identified components of the diet of the Floreana racer on both study sites through the examination of faecal matter. This objective arose as a consequence of its identification during fieldwork. Handled individuals were manipulated to obtain faecal matter, which was later examined for trace particles of identifiable organisms. These particles were then matched to the species or taxa in question and a dietary composition of handled individuals was developed. This information is also useful in the context of translocation, due to the information it provides on the dietary needs and patterns of the species. This information is presented in Chapter 4.

Objective 4. Estimate prey availability on Champion and Gardner-by-Floreana as well as a section of the Floreana coast.

Additionally I developed an estimate of prey density for both study sites, as well as a preliminary investigation into prey density along the Coast of Floreana Island. The Floreana lava lizard (*Microlophus grayii*) is endemic to the Galápagos Islands, and is found on both study sites and is still present on the island of Floreana despite the presence of introduced predators. As part of my research I took measurements of lava lizard density on both study sites for the purpose of comparing the density of Floreana racers and Floreana lava lizards. This information is presented in Chapter 4.

Objective 5. Summarise the relevant threats to the Floreana racer and provide brief recommendations, as well as identify future research needs.

I also provide a summary of the important factors impacting the Floreana racer, under the context of informing a formal (IUCN) assessment for the Floreana Racer. I used research into the factors that contribute to an IUCN assessment as well as information gathered during my field research. IUCN assessments provide valuable information for the effective management of a species (Rodrigues, Pilgrom, Lamoreux, Hoffman, & Brooks, 2006). No IUCN assessment exists for the Floreana racer and, as of early 2017 only 3 members of the *Pseudalsophis* had IUCN assessments. Additionally I present a number of further research needs for this species, based on data collected throughout this study. This information is presented in Chapter 5.

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CHAPTER 2

AN UPDATED MORPHOLOGICAL DESCRIPTION OF *PSEUDALSOPHIS BISERIALIS BISERIALIS*

The author, examining the scale patterns of a Floreana racer on Gardner Islet, off the Coast of Floreana Island.

Photo: Luis Ortiz-Catedral

2.1 ABSTRACT

The Floreana racer (*Pseudalsophis biserialis biserialis*) is a little studied species found in the Galápagos archipelago, with an unresolved regional taxonomy and lacking an updated assessment of conservation status. Some authors recognize three subspecies, based solely on morphological features, whereas others suggest a division into multiple species with non-overlapping distributions. The Floreana racer was first described in 1860 by Günther (1860) based on a single specimen collected on Floreana Island by Charles Darwin in 1835. Van Denburgh (1912) updated the synopsis of the species including a specimen collected on Gardner Islet during the California Academy of Sciences Expedition to Galápagos 1905-1906. More recently, Thomas (1997) reviewed another four specimens from Champion and Gardner Islets to produce the most complete revision of the genus to date. All these studies were based on museum specimens with brief accompanying field notes. To date no researcher has examined live specimens to produce a more detailed description of the colouration range and range of sizes of Floreana racers at their two known remnant populations. In this chapter, I present an updated description for the Floreana racer based on observations in the field of 123 live individuals on Champion and Gardner Islet. This component of my thesis provides new data to further assess the taxonomy of *Pseudalsophis* and to better understand the morphological variability of this island-dwelling genus.

2.2 INTRODUCTION

The Floreana racer (*Pseudalsophis biserialis biserialis*) is one of six species of terrestrial snakes traditionally recognized in the archipelago together with the Española racer (*P. hoodensis*), Banded Galápagos racer (*P. slevini*), Striped Galápagos racer (*P. steindachneri*), Central Galápagos racer (*P. dorsalis*), Western Galápagos racer (*P. occidentalis*) (Thomas, 1997; Zaher et al., 2009). As mentioned in Chapter 1, *Pseudalsophis biserialis* traditionally divided into two sub-species: *biserialis* (Floreana racer) and *eibli* (San Cristobal racer). Historically, the Galápagos terrestrial snakes have been placed in various genera within the family Colubridae; subfamily Xenodontinae including, *Pseudalsophis*, *Phylodryas* and *Antillophis* (Thomas, 1997; Zaher et al., 2009). The morphology of the hemipenis indicates a close relationship to *Alsophis*, but mitochondrial and nuclear DNA analysis support its placement in the genus *Pseudalsophis* (Zaher, 1999; Zaher et al., 2009). A recent phylogenetic analysis however, places *Pseudalsophis* in the family Dipsadidae, not Colubridae (Grazziotin et al., 2012). The numerous taxonomic changes highlight the puzzling nature of these reptiles.

Based on the analysis of Thomas (1997), the Floreana racer is one of three subspecies: *Pseudalsophis biserialis biserialis* ("Eastern Galápagos racer" or "Floreana racer"; Islets off the coast of Floreana, and San Cristobal); *P. biserialis dorsalis* ("Central Galápagos racer"; Santa Cruz, Santiago and Santa Fe) and *P. biserialis occidentalis* ("Western Galápagos racer"; Isabela and Fernandina). Thomas (1997) did not recognize the San Cristobal subspecies and lumped both Floreana and San Cristobal racers under a single species. Altamirano (2008, *in litt.*) suggests that there are enough morphological differences, and possibly genetic differences between *dorsalis* and *occidentalis* to warrant their classification as separate species as later discussed by Zaher et al. (2009). In this thesis I follow the separation suggested by Mertens (1960), and consider the Floreana racer and San Cristobal racer separate subspecies.

Understanding the taxonomic boundaries in this group of snakes is important, first to determine their geographic distribution and outline their evolutionary history, and second to assess their conservation needs. This in turn can be applied to identify and implement management interventions aimed at improving the conservation status of specific taxa in well-defined geographic regions. While numerous studies integrating information from morphological analysis and molecules have advanced our understanding of the evolutionary history and population genetics of Galápagos finches (Burns, et al., 2002); mockingbirds (Arbogast et al., 2006); tortoises (Caccone et al., 1999); iguanas (Tzika et al., 2008; Steinfartz et al., 2009); native rats (Johnson, 2009) and lava lizards (Benavides et al., 2009), Galápagos terrestrial snakes have remained an elusive subject to study integrating morphological and molecular analyses. This situation represents a significant gap in our understanding of the evolution and diversification of vertebrates in the Galápagos Islands.

Günther (1860) first described the Floreana racer based on a single specimen collected by Charles Darwin in 1835 on Floreana Island, and currently at the British Museum of Natural History (Fig. 2.1). Further specimens were collected on Champion and Gardner-by-Floreana (both islets off the coast of Floreana) and San Cristobal during the expedition by the California Academy of Sciences (Van Denburgh, 1912). Galápagos racers can still be found in the later localities, but the only evidence of their existence on Floreana Island is the collection by Darwin. The 1905-1906 California Academy of Sciences failed to record or collect any snakes on Floreana Island after 28 days of searches (Steadman, 1986). Van Denburgh (1912) was the first to suggest, "*It is probable that the ravages of the smaller kinds of mammals that have been introduced (…) –particularly rats and cats- have pushed (the snakes) to the verge of extinction"*. Recent efforts to find Galápagos racers on Floreana Island have failed also after 15 days of intense vertebrate surveys in 2011 (Jimenez and Ortiz-Catedral, unpublished). Nevertheless, there is a slim chance that Galápagos racers are still present, in very low densities on the island of Floreana. Determining whether or not this is the case, requires further field surveys in potential habitat patches. This is not a trivial matter since a remnant population of Galápagos racers on Floreana Island is likely to harbour unique haplotypes (DNA sequence variations), that can contribute to the long-term conservation of the species, as exemplified by a study on the haplotype diversity of Floreana mockingbirds (*Mimus trifasciatus*) (Hoeck et al., 2010). As mentioned in Chapter 1, the reintroduction of the Floreana racer back to Floreana Island, is currently considered as part of the management agenda by the Directorate of the Galápagos National Park. Thus, clearly understanding the taxonomy of the Floreana racer is relevant in this context.

In general, the taxonomy of snakes is problematic. Morphological studies remain an important approach for identifying and classifying species (Will & Rubinoff, 2004) despite the advancement of genetic studies for establishing the relationships between different populations or taxa (Takezaki & Nei, 1996). Morphological studies are a necessary component of biological studies and allow for the identification of future research priorities (Weins, 2004). Morphological studies on snakes focus on a number of characters including scale series, total size and even weight (Arnold, 1983). The scale series, particularly those of the head are of special interest as part of morphological studies (Clark & Inger, 1942) partly because genetic and developmental factors can lead to overlapping scale series (Dohm & Garland, 1993). Several authors have suggested that these scale series are under selection pressures (Arnold, 1988; Fox, 1975), while others have implied that they are not (Snell, Snell, & Tracy, 1984; Travis, 1989). A recent study comparing the scales series between mainland and island populations of the tiger snake (*Notechis scutatus*), found that the island species have, on average, a greater number of supra-labial scales as well as mid-body dorsal scales (Fabien, Bonnet, Maumelat, Bradshaw, & Schwaner, 2004). The authors link these differences to the differences in diet: the island population feeds on larger prey items than their mainland dwelling counterparts. This study highlights the importance of scale counts as a component of morphological studies, the potential exists that the study of scale series will highlight further avenues of research.

The most comprehensive review of the morphological variation among Galápagos snakes is by Thomas (1997), based entirely on the examination of museum specimens. By examining the morphological characteristics, such as scale counts and hemi-penis morphology, in conjunction with the locations of capture, Thomas discussed the range of morphological variation found in museum specimens, and suggested taxonomic sub-divisions for each sampled taxa including the Floreana racer.

Figure 2.1. Holotype of *Pseudalsophis biserialis biserialis* collected by Charles Darwin in 1835, and currently at the Natural History Museum, London. Specimen catalogue number 1895446.

Photo: L. Ortiz-Catedral

In this Chapter, I present an updated description of the Floreana racer based on observations from live individuals in the field. Thomas (1997) revision and description of the Floreana racer (or “Eastern Galápagos Racer” as he names it) is based on the examination of only five museum specimens: two from Champion, two from Gardner and one (Holotype) from Floreana Island. The examination of multiple live specimens that I present here allows for an updated description of this taxa, underrepresented in museum collections, and a better understanding of its morphological variability. I also discuss the measurable morphological differences between snakes from Champion and Gardner Islets.

2.3 METHODS

I collected morphological data from individuals captured by hand on the islets of Champion and Gardner (see Chapter 3 for details on capture methods). For the synopsis of the Floreana racer, I counted nine scale series on each individual, four head scale series and five-body scale series. The four head scale series include: supra-labial scales, infra-labials, post-oculars and temporal (Fig. 2.2). The five series of body scales include: scale rows posterior to the head; scale rows in the mid-body section; and scale rows anterior to the cloaca or vent; ventral scales, and sub-caudal scales (from the vent down to the end of the tail) (Fig. 2.2). Other morphological data collected includes weight; Snout to Vent Length (SVL) and Tail length (TL), and girth in the mid-section. The length of individuals was measuring using a piece of string. One end of the string was placed over the snout of the snake until the end of the string was aligned with the most anterior end of the snake’s face.

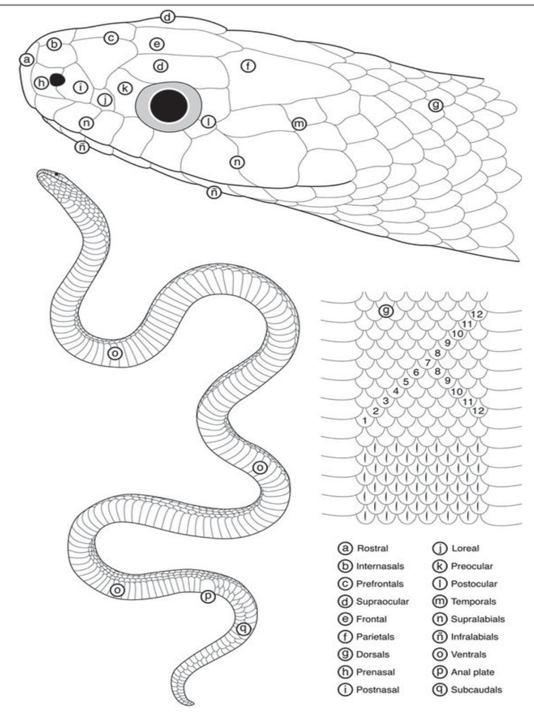

Figure 2.2. A schematic representation of scale series in snakes. Image used with permission from tropicalherping.com

The string was then used to measure the body of the snake by placing the string against the body in increments to ensure that the movement of the snake did not affect the measurement. A mark was then made on the string corresponding to the position of the vent, and measurements were continued down to the posterior end of the tail. The string was then measured against a ruler to obtain the relevant value. Due to the errors associated with the measurements of snakes (Luiselli & Randa, 2005), an additional method to obtain length measurements was used: individuals were placed in the bottom of a clear plastic container and a piece of foam was placed over them, gentle pressure was then applied so the snake did not move, a marker was then used to trace the outline of the snake on the bottom of the plastic container. The snake was then removed from the box as the line was measured. The weight of individuals was measured in the field using PESOLA® spring balances to the nearest gram.

Head length and width were measured with callipers. The head length was measured from the tip of the snout to the posterior end of the last supra-labial scale (see Figure 2.3). The head width was measured at the widest point of the head (Figure 2.3). These morphological characters were also measured on recaptured individuals. Girth was only measured on individuals captured from November 2016 onwards. Girth was measured by placing a tape measure around the widest point (mid-section) of the individual.

Standardized photos were also taken of handled individuals. The purpose of these photos was to examine the colour and pattern variation between individuals and islets. I compared the differences in morphological traits between populations using one-way ANOVA in StatView V. 5. Data are presented as means ± SD.

Figure 2.3. Examples of head length (left) and width (right) measurements on Floreana racers using a calliper.

2.4 RESULTS

A total of 123 individuals were captured, weighed and measured during this study: 103 on Gardner-by-Floreana and 20 on Champion. The original dataset is presented in Appendix 1. These field data were used to elaborate an updated diagnosis of the Floreana racer.

***Subspecies diagnosis**:* Dorsal colour pattern spotted; pairs of spots along the dorsal surface, gradually reducing towards the tail. Tail tip brown or reddish brown. Venter cream, with pigmented spots, iridescent in live specimens. Overall colouration light grey to brown, with pale nuchal spots. Ventral scales 194-231; Sub-caudals 82-132; Head length 7-25.9 mm; Head width 5.2-25.3 mm; Total length 157.4 – 1290 mm; Snout-Vent length 225-967 mm; Tail length 80-370 mm; Supralabials 6-9, with either IV, IV-V, IV-VI, or V-VI entering the orbit; Infralabials 8-11; Post-ocular scales 1-4; First temporal series 1-3; Second temporal series 2-4; Third temporal series 2-4; Girth 14-68 mm. Dorsal scales posterior to the head 15-20; Dorsal scales in the mid-body section 14-19; Dorsal scales anterior to the vent 13-18.

An example of the range of colouration is presented in Fig. 2.4

Figure 2.4 Examples of the range of colouration in Floreana racers. Left: light grey individual from Gardner-by-Floreana; Right: brown individual from Champion Islet.

The majority of individuals sampled (85; 69%) were symmetrical for their post-ocular, supralabial and infralabial scale series. The infralabial scale series was most commonly asymmetrical (21; 17%); followed by the supralabial scale series (14; 11%) and post-ocular scale series (5; 4%).

I detected differences in morphological traits between the two populations sampled in this study. On Gardner-by-Floreana, Floreana racers are significantly longer than on Champion (Total length Champion 681.80 ± 162.83 mm (n=20); Gardner-by-Floreana 804.83 ± 192.10 mm (n=103); F= 7.19; *P*=0.008; SVL Champion 492.05 ± 121.03 mm (n=20); Gardner-by-Floreana 577.41 ± 137.24 mm (n=103); F= 6.71; *P*=0.01). Floreana racers on Gardner-by-Floreana also have longer tails than individuals on Champion (Tail Length Champion 189.75 ± 47.09 mm (n=20); Gardner-by-Floreana 230.82 ± 52.37 mm (n=103); F= 10.62; *P*=0.001). Finally, on Gardner-by-Floreana, Floreana racers exhibit a larger girth than on Champion (Girth Champion 3.28 ± 1.89 mm (n=6); Gardner-by-Floreana 4.4 ± 1.16 mm (n=41); F= 4.09; *P*=0.05).

The number of ventral and subcaudal scales did not differ significantly between Gardner-by-Floreana and Champion (Champion 205.4 ± 3.95 ventrals (n=20); Gardner-by-Floreana 206.93 ± 5.77 ventrals (n=103); F= 1.28; *P*=0.26; Champion 109 ± 0.5 subcaudals (n=20); Gardner-by-Floreana 111.97 ± 9.21 ventrals (n=103); F= 1.67; *P*=0.20). Similarly, the mass of Floreana racers did not differ significantly between populations (mass Champion 50.97 ± 55.79 g (n=20); mass Gardner-by-Floreana 71.80 ± 52.75 g (n=103); F= 2.55; *P*=0.11). Lastly, Floreana racers on Gardner-by-Floreana showed longer heads than on Champion (Head length Champion 13.07 ± 4.52 mm (n=20); Gardner-by-Floreana 18.59 ± 3.82 mm (n=103); F= 32.78; $P <$ 0.001), but the head width between populations did not vary significantly

(Head width Champion 12.63 ± 5.67 mm (n=20); Gardner-by-Floreana 11.31 ± 3.24 mm (n=103); F= 2.109; *P* = 0.15).

2.5 DISCUSSION

The species description provided by this study builds on the previous species descriptions by Güther in 1860, Van DenBurgh in 1912 and Thomas in 1997. The intial work of Güther was based on a single specimen collected by Charles Darwin (Güther, 1860). Later, Van DenBurgh examined a speciemen collected as part of the California Academy of Sciences expedition to the Galápagos in 1905, as well as the individual previously described by Güther (Van Denburgh, 1912). Thomas (1997) diagnosis of the species included five individuals but no field observations (Thomas, 1997).

In this study, I examined the morphological traits of 123 individuals in the field. My study indicates that the morphological variability of the Floreana racer is greater than represented in Museum collections for this taxon. In his treatment of the Galápagos terrestrial snakes, Thomas provides a key to the different species. According to this key, the Floreana racer can be separated from other species in the archipelago by presenting 190-210 ventral scales, 2 or rarely 3 postocular scales; a dorsal scale row anterior to the vent with 15 scales (Thomas, 1997). In this study I show that Floreana racers present 194-231 ventral scales, 1 to 4 postocular scales and a dorsal scale row anterior to the vent with 13-18 scales. These findings highlight the value of field studies on live specimens to better delimit morphological variability among taxa, and to develop accurate taxonomic keys for the Galápagos terrestrial snakes.

The specimens examined for the diagnosis of the species prior to this study, have been preserved in ethanol and potentially other preservative agents to halt decomposition (Pesantes, 1994). This treatment can alter the tissues, affecting morphological characteristics such as weight and length in the preserved specimens (Shields & Carlson, 1996). Thus, a further advantage of my study is that it presents for the first time the range of lengths and weights for this little studied taxon.

This study also provides the first ever comparison of Floreana racer populations between the islets of Champion and Gardner. Until the work of Thomas the only specimens collected were from Floreana Island or Gardner islet. The individuals on Champion islet were designated to the Floreana species due to the proximity of Champion islet to Floreana. The California Academy of Science was never able to obtain a Floreana racer sample from Champion islet (Van Denburgh, 1912).

In my study, I registered predominantly symmetrical individuals for at least one of the measured scale series (see Results). Scale counts can be indicators of genetic factors, growth factors or provide insights into different dietary conditions (Dohm & Garland, 1993; Fabien et al., 2004; Löwenborg & Hagman, 2016). The difference in scale counts between individuals has been linked to possible genetic variation between individuals (Dohm & Garland, 1993). Differences in scale counts have also been linked to differences in diet between two populations (Fabien et al., 2004). Other scale differences have been linked to different thermal factors during incubation, resulting in uneven ribs and the corresponding ventral scales (Löwenborg & Hagman, 2016).

These studies have all focused on a different causal factor for the difference in scale counts.

A key limitation of this study is the inability to accurately state the sex of each individual. All previous studies have relied on the hemi-penis structure to determine the sex of the specimen. The structure of the hemi-penis is a common measure of the sex of individuals and is use of a large number of snake species (Jenner & Dowling, 1985). The examination of the hemi-penis structure was not a part of this study, and as such it is not possible to accurately state the sex of any individuals, the sex of individuals can also be determined through DNA methods, however the use of DNA sampling was not included as part of this study (see Chapter 5 for more information). This is a limitation of these results due to their inability to determine if there are any patterns of sexual dimorphism, in either size, colouration or scale counts.

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CHAPTER 3

POPULATION STATUS OF THE FLOREANA RACER ON THE ISLETS OF CHAMPION AND GARDNER-BY-FLOREANA

A Floreana racer (*Pseudalsophis biserialis biserialis*) on Gardner Islet, off the Coast of Floreana Island.

Photo: Jenny Daltry

3.1 ABSTRACT

The Floreana racer, formerly widespread in the lowlands of Floreana Island is now restricted to the Islets of Champion and Gardner-by-Floreana. Scientists have known of the existence of these populations since the early 1900’s, but prior to this study there has been no attempt at determining their population size and status. Floreana Island is undergoing a major ecological restoration that includes the repatriation of 13 locally extinct animal species, including the Floreana racer. I conducted a population estimate on these islets as a first step to develop a translocation strategy for the Floreana racer. I captured and measured a total of 123 individual snakes, of these 119 were large enough to implant a PIT tag to allow for individual identification; the other four were marked by clipping scales. I used a mark-recapture method to estimate population size. Only 14% of captured individuals were recaptured. On Champion I estimate there are up to 209 individuals whereas on Gardner-by-Floreana there are up to 2879 individuals. One limitation of these estimates is that it is biased towards larger individuals (i.e. sub-adults and adults), which are easier to detect and capture. My study provides the first population assessment for translocation planning of the Floreana racer back to its namesake island.

3.2 INTRODUCTION

Determining the size of animal populations is an active area of research in conservation biology. Low numbers of individuals can trigger emergency interventions to increase population size, and population growth can be used as a parameter to quantify conservation success. For instance, the historically abundant Puerto Rican parrot (*Amazona vittata*) declined to 13 individuals by the 1970's, a situation that prompted intense captive breeding and artificial nest management to increase parrot numbers (Snyder *et al.*, 1987). By 2011, the population size of Puerto Rican parrots is estimated at 50-80 individuals (BirdLife International, 2016). Although the population recovery of the Puerto Rican parrot can be considered moderate, it serves as an example to illustrate the ongoing need to understand changes in populations of animals of conservation interest, whether these changes are apply to local species of the global distribution of a given taxon (Whittaker, 1972).

Research on animal populations extends beyond the apparent management needs for small populations. Biologists are also interested in developing and refining methods to estimate population numbers. During the 1970's there was a significant development of methods to estimate animal abundance, based on the marking of a subset of individuals from a population, their release and subsequent recapture (Seber, 1982). Collectively, these methods are known as "capture-recapture" (Begon, 1979). Other methods to estimate population sizes have been developed and do not require the physical marking of subsets of individuals, these include distance sampling, trapping, point-count, and road sampling (Anderson, Burnham, White, & Otis, 1983; Howell, 1951). Broadly, these methods aim to provide an overview of the population status of a given taxa, based on the accessible records of a subset of individuals available for analyses.

In practice, methods to estimate animal populations are often complementary: distance sampling, when coupled with point counts, for example, is effective to quantify bird species, because observers can register birds calls as part of the sampling process (Simons, Alldredge, Pollock, & Wettroth, 2007; Somershoe, Twedt, & Reid, 2006). This approach however, is clearly unsuitable for animals that do not vocalise or produce calls at regular intervals. Given that different taxa pose different challenges for population studies, taxon-specific methods have been adapted for a range of arboreal species, bird species and even plant species (Carey, Biswell, & Witt, 1991; Elizinga, Salzer, & Willoughby, 1998; Manuwal & Carey, 1991).

As discussed in Chapter 1, there are comparatively fewer field studies on snakes than in other vertebrate groups. This situation applies also to population studies. In general, the groups of methods to estimate animal abundance referred to above, can also be applied to the study of snake populations. The perception by many researchers it that the secretive nature of snakes makes them difficult to study (Dorcas & Wilson, 2011). While this might be the case for many species, some snake species are very conspicuous. For example, a number of European vipers (e.g. *Vipera berus* and *Vipera aspis*) emerge from their winter burrows and engage in assemblage mating (see Chapter 1), knowledge of these annual events can assist in the development of population studies, as numerous individuals are accessible for capture and marking (Bonnet & Naulleau, 1996).

Snake populations can also be studied along roads. In its most basic form, road sampling allows the visual detection of snakes along segments of known size and the opportunity to obtain basic biological information from individuals captured (Rudolph, Burgdorf, Conner, & Schaefer, 1999). One limitation of road sampling is that it underperforms when dealing with territorial species or nesting individuals as their chances of detection are lower than that of individuals moving freely within the study area (Steen & Smith, 2006).

Another approach to study snakes, particularly dangerous snakes, is distance sampling, which does not require handling of individuals (Rodda & Campbell, 2002). A key element of distance sampling is ability of observers to effectively identify every individual along a pre-selected transect (Lukcas, Kisslings, Reid, Gende, & Lewis, 2010). Distance sampling also assumes that each individual is only counted once during sampling. These requirements can make distance sampling very restrictive in some field situations. A recent study was undertaken to investigate the ability of distance sampling to accurately measure the population density of a dune-dwelling Sagebrush lizard (*Scleoporus arenicolus*) in New Mexico. The authors concluded that the use of distance sampling, when compared to other sampling methodologies, was unreliable and underrepresented the true density of lizards within the study site (Smolensky & Fitzegerald, 2010).

The use of artificial cover objects is another common method that is used for the investigation of snakes and other herpetofauna. This method takes advantage of the reclusive nature of snakes, and has been used widely in field situations (Joppa, Williams, Temple, & Casper, 2009). Using artificial cover objects to study snakes reduces the impact of searching on natural cover objects, resulting in a reduced impact on ecosystem composition (Engelstoft & Ovaska, 2000; Scheffers, Mcdonald, Hocking, Conner, & Semlitsch, 2009). Artificial cover objects however, have a number of limitations, for example, they are heavily reliant on the weather conditions. An experiment examining artificial cover objects found that snakes were most commonly encountered during the cooler periods of the year. The artificial cover objects absorbed heat more readily than the natural substrata, allowing snakes to thermoregulate more effectively (Engelstoft & Ovaska, 2000). A further limitation of artificial cover objects is that certain species prefer different materials. Thus providing a potential barrier to the effectiveness of any chosen artificial cover objects (Engelstoft & Ovaska, 2000; Hampton, 2007).

One further alternative for the study of snakes is the use of traps and drift fences (Greenberg, Neary, & Harris, 1994). Traps and drift fences are used in conjunction to corral individuals towards the traps where they can be collected at a later time. This method is particularly useful to study snakes, due to their inability to scale smooth vertical barriers (Saenz, Collins, & Conner, 1999). Nevertheless, traps and drift fences can be impractical in some field situations, where the substrate is too hard for the set-up of fences, for instance small volcanic islands.

The methods described above can be implemented on remnant populations as well as populations established via translocation (i.e the intentional release of animals to the wild in the attempt to establish, re-establish or augment a population (Griffith, Scott, Carpenter, & Reed, 1989)). Translocations have become a central element in conservation of threatened species such as the Kakapo (*Strigops habroptilus*) and Hihi (Stitchbird, *Notiomystis cincta*) (Armstrong, Castro, Alley, Feenstra, & Perrott, 1999; Clout & Merton, 1998). In general herpetofauna translocations occur less frequently (Miller, Bell, & Germano, 2014), but there have been significant advances in recent years (Germano, Ewen, Mushinsky, McCoy, & Ortiz-Catedral, 2014). Reptiles are an important part of ecosystems and are essential for the restoration of damaged ecosystems. Several successful reptile translocations have been made in New Zealand with a number of skink species (*Cyclodina alani*, *C. oliveri*, *C.whitakeri* and *Oligosoma suteri*), these species were identified as priorities for conservation management through a thorough understanding of their individual status' (David R. Towns & Ferreira, 2001). In New Zealand between the years of 1984-2008 there were 74 translocations of herpetofauna species, in contrast to 70 avian translocations taking place between the years of 1980 and 1990 (Miller et al., 2014; Miskelly & Powlesland, 2013). While, herpetofauna translocations are less common they are increasingly necessary for the management of threatened taxa (D.R. Towns, Miller, Nelson, & Chapple, 2016).

In the Galápagos Islands, there is a long tradition of reptile translocations. Land Iguanas (*Conolophus subcristatus*), and Giant Tortoises

(*Geochelone* spp.) have been repatriated to historical locations following captive breeding (Milinkovitvh et al., 2004; Tzika et al., 2008). In the near future, numerous translocations of various taxa are contemplated to various islands in the Galápagos archipelago as more and more sites are restored following the eradication of invasive species (Barnett, 1986; Campbell, Donlan, Cruz, & Carrion, 2004; Carrion, Donlan, Campbell, Lavoire, & Cruz, 2007; Cruz, Donlan, Campbell, & Carrion, 2005). Among these species is the Floreana racer, identified as a candidate species for reintroduction to Floreana Island following the eradication of invasive predators (Conservation, 2013). The Floreana racer has been locally extinct on Floreana Island since the late 1800's possibly due to the combined effect of fires, and invasive rats and cats (Steadman, 1986; Thomas, 1997; Van Denburgh, 1912). The evidence of the historical presence of this species on Floreana Island comes from sub-fossil bones (Steadman, 1986) and a single specimen collected on Floreana Island by Charles Darwin (Fig. 2.1, Chapter 2) (Thomas, 1997).

In this Chapter, my aim was to provide the first population estimates of the Floreana racer on the only two known populations on Champion and Gardner-by-Floreana.

3.2 METHODS

A number of possible methods to estimate the population size of Floreana racers were considered in the preliminary stages of this project. Given that access to the islets would be restricted and it would only be possible to safely transport a limited amount of field equipment careful consideration was made to the materials needed for a given method and how much equipment would be necessary to obtain suitable results. The use of roads a survey method was immediately dismissed, due to the lack of tracks on the island, and the associated prohibitive cost of setting up tracks for this project.

The use of either trapping/drift fences or artificial cover objects was dismissed, as these methods require the transport and installation of a large amount of materials on the two small study islets. A trapping regime would require the design of suitable traps capable of capturing Floreana racers without the addition of other less desirable species such as Darwin Scolopendras, or centipedes (*Scolopendra galapagoensis*). These centipedes can grow to 30 cm long, and are known predators of juvenile Floreana racers (Ortiz-Catedral, pers. obs.). Pitfall traps were also dismissed due to the volcanic nature of the soil, which limits the potential sites where traps could be placed. Further, heating up of traps was also identified as a concern for this method. Researchers in Australia have previously investigated the effects of temperature within pit and funnel traps and found that temperatures can reach lethal levels for small species within a day (Thompson & Thompson, 2009). While it is unlikely that any Floreana racers would of remained in a trap for over a day it is still probable that individuals exposed to high temperatures, without any respite, would suffer cellular damage.

Artificial cover objects were also deemed unsuitable for this study. Numerous studies have investigated the preferred material for artificial cover objects and the optimal size (Engelstoft & Ovaska, 2000; Hampton, 2007;

Joppa et al., 2009). Due to the unknown distribution patterns of Floreana racers, it was not possible to determine the best type of material to use or the most suitable locations for the placement of these artificial cover objects.

Distance sampling was also considered as a methodology to estimate density of Floreana racers. However previous research has shown that the critical assumptions of distance sampling are not well suited to reptilian species (Rodda & Campbell, 2002). Particularly the assumption that 100% of animals along the transect will be detected. Many reptiles remain inactive for extended periods of time, and are often camouflaged against the environment due to their method of obtaining prey through ambush hunting (Ayer & Shine, 1997). Thus it is very difficult to guarantee that every individual would be identified during sampling.

After consideration of these methods, and consulting with colleagues I implemented a closed population mark-recapture method using daylight searches for Floreana racers. A similar approach has been used for the Antiguan racer (*Alsophis antiguae*) (J. C. Daltry et al., 2001) and the Saint Lucia racer (*Erythrolamprus ornatus*) (Williams, Ross, Morton, Daltry, & Isidore, 2016). Mark-recapture methods, require the capture of individuals, a unique mark or tag, and recapture of a subset of marked individuals. This method can be used to determine the size of the population; it also provides data on the survivability of certain individuals and can be used to gather morphological or physiological data on handled individuals (Pradel, 1996). Mark-recapture methods are used on a wide variety of species due to the basic nature of the sampling methodology, and are often used on snakes due to their reclusive nature. Mark-recapture methods allow for the collection of multiple types of data, thus maximizing the information gathered through the rare encounter of a secretive species. The key assumption of closed population mark-recapture methods is that over the course of the study there are no births or deaths within the population, also that there is no immigration of emigration and that all individuals are equally likely to be captured (Pradel, 1996). These assumptions are ideally suited to island dwelling species, especially species that cannot freely travel between islands, such as snakes (J. C. Daltry et al., 2017; Williams et al., 2016).

Daylight searches for Floreana racers commenced approximately at 5:30 h and continued to 10:00 h, then resumed at 14:30 h and continued until 18:30 h over 29 field days, totaling approximately 230 sampling hours. The search team consisted of three to five observers walking on the accessible trails and open areas on Champion and Gardner-by-Floreana (see Chapter 1 for a habitat description of study sites). Observers attempted to capture every snake encountered by hand, these were then placed in cotton pillowcases. Every snake captured was measured and weighed with a precision scale balance (Pesola®) (See Chapter 2 for details on measurements). Capture locations were geo-referenced with a hand held GPS (Garmin® *GPSmap* 62S).

To mark snakes I implanted a 12 mm Passive Integrated Transponder (PIT) tag (TROVAN®) subcutaneously in the either the left or right flank, approximately 2 cm anterior to the vent. I only tagged individuals longer than 30 cm. Processing of each captured snake took approximately 29 minutes (n=51). Smaller individuals were marked by clipping ventral scales.

I analysed mark-recapture data using Begon's weighed mean estimator (Begon, 1979):

$$N = \frac{M_i n_i}{(\sum m_i) + 1}$$

Where M_i is the number of marked snakes at large in the population on day *i,* n_i is the number of snakes caught on day *i*, and m_i represents the number of marked snakes caught on day *i*. The standard error calculation for this mean estimator is given by:

$$N_x = \sqrt{\frac{1}{\sum mi + 1}} + \sqrt{\frac{2}{(\sum mi + 1)2}} + \sqrt{\frac{3}{(\sum mi + 1)3}} + \sqrt{\frac{4}{(\sum mi + 1)4}}$$

Other demographic studies on island snakes have used this estimator also as the data better fits the field situation of my study species: closed population, no immigration or emigration during the study period, no deaths or hatching of individuals and an equal probability of catching all Floreana racers (J. C. Daltry et al., 2001; Williams et al., 2016). I excluded recaptures within the first 48 h following release (n= 2), because Floreana racers, like other island racers (see Williams et al., 2016) tend to stay within release area for a couple of days. We aimed to search for Floreana racers under similar weather conditions. Most sampling days were sunny and still, with a couple of overcast and windy days. I completed analyses in excel (Begon's weighed mean) and StatView Version 5 (Linear regressions, descriptive statistics).

3.3 RESULTS

The team of observers and I captured, weighed and measured a total of 123 Floreana racers on both islets. On Champion Islet, only 20 individuals were captured, another four were encountered but could not be captured. On Champion Islet the combined effort of all observers yielded 352 man-hours of searches, and a mean encounter rate of 0.07 Floreana racers/h (i.e. 20 captures plus four encounters only). On Gardner-by-Floreana we captured 103 Floreana racers.

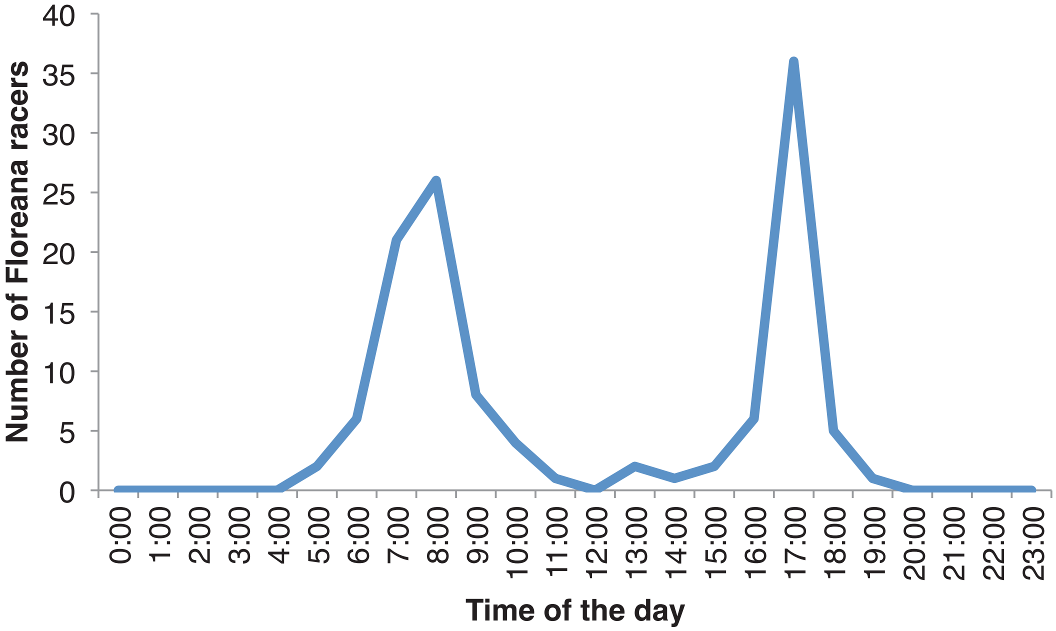

Figure 3.1 Floreana racer captures per time of the day on Champion and Gardner-by-Floreana.

Another nine individuals escaped and could not be captured. The total search effort was double the effort on Champion and equivalent to 704 man-hours of searches, and a mean encounter rate of 0.16 Floreana racers/h (i.e. 103 captures plus nine encounters only). Overall, the areas of higher captures were at 8:00 h and 17:00 h (Fig. 3.1).

Begon's weighed mean estimate of population size for Champion islet is 92 ± 117.28 individuals; this estimate is based on a single recapture, therefore this estimate is inaccurate. Assuming that the racers not captured indeed represent different individuals the total population size on Champion would be 24 to 209 Floreana racers, or 2.5-22 racers/ha. For the study area on Gardner-by-Floreana (see Chapter 1) Begon's weighed mean estimate of population size is 338.53 ± 87.23 individuals, or approximately 21 to 45 Floreana racers/ha (lower and upper estimates), based on 16 individual recaptured. Extrapolating this value to the total area of Floreana racer habitat on Gardner-by-Floreana (81 ha), the total population size of Floreana racers ranges from 1701 to 2835 Floreana racers. Combined, these estimates give a global population for this subspecies of 1722 to 3044 individuals.

The number of days between captures and first re-capture (including <48 hours recaptures) is 187.14 days (range 2 – 365 days) on both islets. The locations of capture of Floreana racers is presented in Fig. 3.2. During the sampling period, recaptured individuals (including <48 hour recaptures) moved approximately 170.15 m on average (range 21.7-386 m) (i.e. distance of recapture location-capture location).

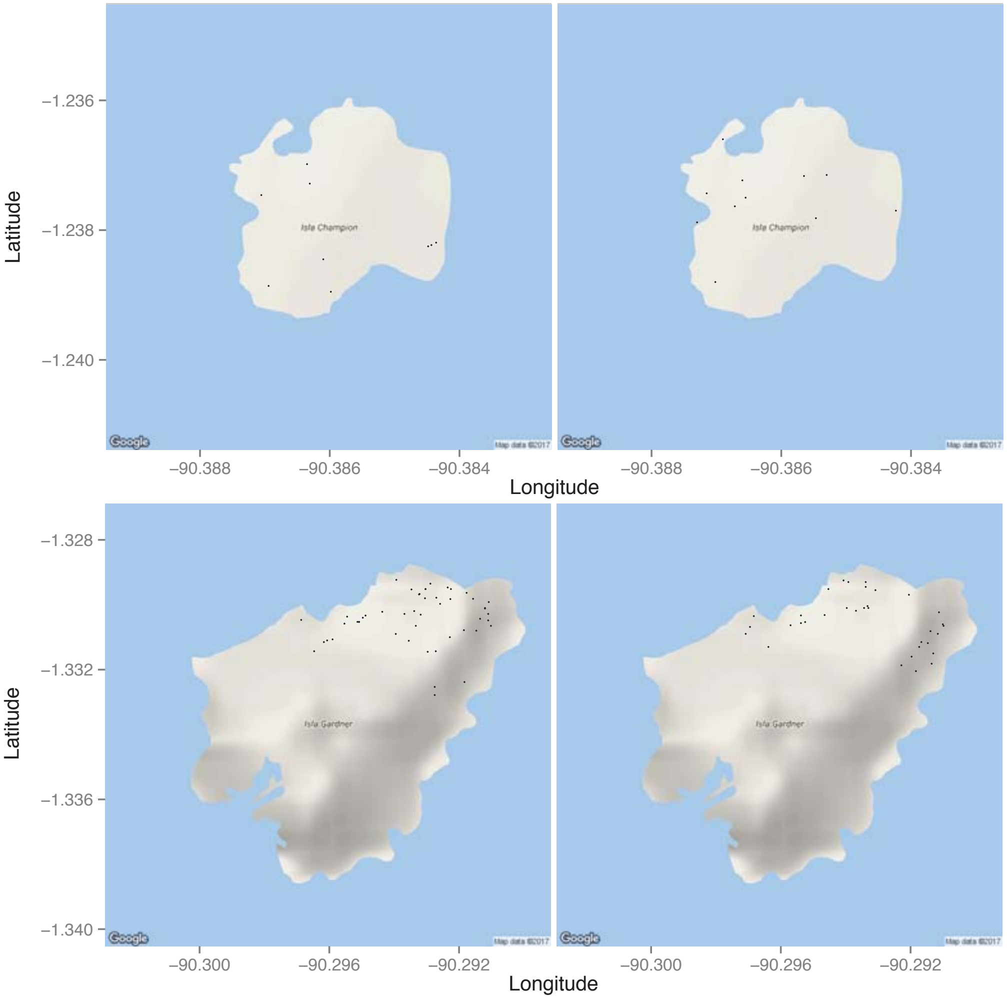

Figure 3.2 Capture locations of Floreana racers on Champion (above) and Gardner-by-Floreana (below). Right panels 2015-2016 sampling period; Left panels 2016-2017 sampling period.

Recaptured individuals showed non-significant changes in mass. On average, the change in body mass was 0.37 ± 3.72 g (Linear regression Y = -5.124 + .028 * X; R^2 = .128; F = 1.61, *P* = 0.23; n = 13). Similarly, recaptured individuals showed non-significant difference in distance travelled between capture and recapture up to 365 days after (mean 169.78 m; range 21.7-386 m; n = 13) (Linear regression Y = 70.725 + .423 * X; R^2 = .205; F = 2.32, *P* = 0.16; n = 13) (Fig. 3.3; Table 3.1).

3.4 DISCUSSION

Estimating the population size of snake populations on small islands requires intensive searches. My study represents the first systematic attempt at estimating the global population size of the Floreana racer, a subspecies endemic to Floreana Island (where it is now extinct) and two islets off the coast of Floreana: Champion and Gardner-by-Floreana. My study indicates that the densities of Floreana racers on these islets is different with approximately twice the density of racers on Gardner-by-Floreana than on Champion. The densities of snakes encountered on Champion are roughly comparable to similar-sized islands in the West Indies. For instance, on York and Great Bird islands (7 and 8.4 ha respectively) there are approximately 126 and 169 Antiguan racers (Daltry et al., 2017). On 12 ha Maria Major, Williams et al. (2016) report approximately 50 Sain Lucia racers. Currently there are no population estimates for other racer populations in the Galápagos Islands. Based on the information provided by Altamirano (1991), I calculated an encounter rate of 0.29 snakes/h for Espanola racers (*Pseudalsophis hoodensis*). Although that study looked at snake behaviour and not their population size, from the results presented it appears that the population of Espanola racers occurs at a higher density than Floreana racers.

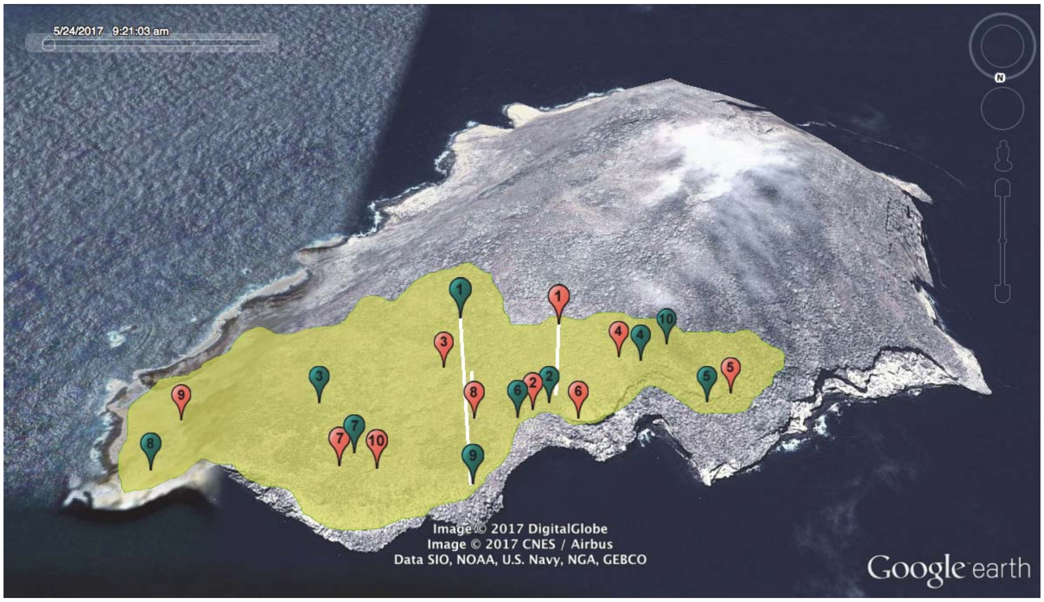

Image © 2017 DigitalGlobe
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Data SIO, NOAA, U.S. Navy, NGA, GEBCO

Figure 3.3 Capture and recapture locations for ten Floreana racers on Gardner-by-Floreana. Red markers indicates sites of Initial Capture, Green markers Indicate sites of Recapture. The area in light yellow represents the study area (17 ha). See Table 3.1 for more detail.

Table 3.1 Dates of capture/recapture for ten Floreana racers and estimated linear distance travelled between events.

Code	Racer ID	Date of Initial Capture	Date of Recapture	Days to recapture	Distance travelled (m)
1	GAM	7/12/2015	2/12/2016	361	152
2	GCC	30/11/2016	2/12/2016	2	21.7
3	GBZ	11/01/2016	3/12/2016	337	154
4	GAU	7/12/2015	4/12/2016	363	27
5	GCP	2/12/2016	7/01/2016	36	32.3
6	GBL	9/01/2016	8/01/2017	30	69.4
7	GCN	2/12/2016	8/01/2017	37	22.2
8	GBW	10/01/2016	30/11/2016	361	379
9	GAP	7/12/2015	30/11/2016	359	386
10	GAL	7/12/2015	2/12/2016	325	377

Nevertheless this can be explained by the larger study area covered equivalent to 6048 ha (Altamirano, 1991). As indicated in the results section, the estimate of Floreana racers on Champion is based on a single recapture, thus subsequent surveys will yield better estimates (see Chapter 5). Regarding Gardner-by-Floreana, the density of Floreana racers per hectare falls within the range reported for the Antiguan racer on Green Island (Daltry *et al*., 2017).

The assumptions of the Begon's weighted mean model uses to analyse these results are central to the interpretation of my results. The model assumes that all individuals within the population have the same chance of being captured (Begon, 1979). However, as has been previously pointed out on similar species, the probability of capture on juveniles is much lower for individuals under 1 year old (J. C. Daltry et al., 2001). In this study four juvenile Floreana racers were < 30 cm long, and in general, more difficult to catch than larger individuals. This is because of their ability to slip through crevices and lava cracks. While equal catchability of all individuals in a given population is in practice unattainable (Carothers, 1973; Eberhardt, 1969; Wilbur & Landwehr, 1974), the assumption is for it is important to interpret the results and their limitations (Chao, 1987).

Begon's weighed mean also assumes that the methods of tagging do not affect the catchability of the organism. For a number of species however, tagging can affect their recapture (Evans, Lenz, & Gleeson, 1998). It is for this purpose that I chose to use subcutaneous micro transponders. Several methods have been used historically to tag snakes, however, the use of PIT tags is not considered the most suitable option. PIT tags are more expensive than many other methods and unsuited for short-term studies or low-recapture rate species (Winne, Willson, Andrews, & Reed, 2006). However, the alternative methods, such as Heat branding and Freeze-branding require the use of specialized and potentially hazardous equipment (Lewkw & Stroud, 1974). The potential issue with using PIT tags is presence of especially small individuals, who cannot be safely tagged. During my study, 4 individuals, 2 from Gardner and 2 from Champion were deemed too small to receive a PIT tag. Their ventral scales were clipped to ensure that they would remain identifiable in the event of a recapture in the immediate future, but beyond a few months it is uncertain if these marks will be identifiable.

My results also indicate that in terms of catchability, Floreana racers show a bimodal pattern with more captures per hour at 8:00 h and 17:00 h, than during the rest of the day (Fig. 3.1). This bimodal patter is most likely explained by the thermal conditions at the time. The thermal environment was highly influential in determining the number of snakes encounter per hour (Bogert, 1949). On Espanola Island, Espanola racers also exhibit a bimodal pattern of activity, peaking at around 8:00 h and 17:00 h (Altamirano, 1991). The early morning and late afternoon temperatures are lower than the midday temperatures and could possibly provide the optimal thermal factors for metabolism. This finding should be incorporated into future population studies on Galápagos terrestrial snakes and to structure targeted surveys when time and resources are limited.

Floreana racers in my study moved across the study site relative to their original location of capture as shown in Figure 3.3. Individuals GBW, GAL and GAP moved the greatest distance, 377, 379 and 386 m respectively. These individuals represent the greatest distance travelled between capture and recapture. GAM and GBZ moved approximately 150 m from their original site of capture. In general, individuals recaptured shortly after released moved less, GCC was recaptured within two days, and was found 21.7 m from the site of its original capture. Individuals GCP and GCN were both recaptured 37 days after initial capture and moved 32.3 and 22.2 m respectively.

During my study I did not assess habitat quality as a potential factor explaining different densities of Floreana racer per islet. I did however; conduct a pilot study for a rapid assessment of prey availability on Champion and Gardner-by-Floreana, as well as part of the coast of Floreana Island (see Chapter 4). Future studies should quantify the effect of habitat quality on the densities of Floreana racer reported here as this might provide information useful to set conservation targets in the context of the translocation of the species to Floreana Island. My study shows that Floreana racers occur at comparable densities to other islands free of introduced predators (J. C. Daltry et al., 2017; Williams et al., 2016). Introduced predators such as rats (Rattus spp.) and mongoose (*Herpestes javanicus*) are known to deplete snake numbers in the West Indies racers (Jennifer C. Daltry, 2006a, 2006b, 2006c; Jennifer C. Daltry, Anthonyson, & Morton, 2010; J. C. Daltry et al., 2001; J. C. Daltry et al., 2017; Jenny C. Daltry, Morton, Smith, & Sylvester, 2003). In the Galápagos Islands, rats, pigs (*Sus scrofa*) dogs (*Canis familiaris*) and feral cats (*Felis domesticus*) are the culprits for the decline in a range of vertebrate species (Barnett, 1986; Barnett & Rudd, 1983; Coblentz & Baber, 1987; Cruz et al., 2005; Phillips et al., 2011). Thus it is clear that the conservation of the populations of Floreana racer on Champion and Gardner-by-Floreana relies on maintaining these islets free of introduced predators. Since these islets harbour comparable densities of snakes to managed islands in the West Indies, in principle the collection of individuals and their translocation to Floreana Island to establish further populations is warranted, although subject to the upcoming eradication of rats and cats from Floreana Island. For the Antiguan racer, new populations on managed islets ranging in size from 2.1 to 45.2 ha have been established with 14 to 46 individuals (Daltry *et al*., 2017). Given that the Champion and Gardner-by-Floreana populations of the Floreana racer fall within the range of source populations for Antiguan racers, I suggest that a similar strategy can be developed for this Galápagos endemic, in order to re-establish it to its historical range.

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CHAPTER 4

DIET OF THE FLOREANA RACER AND ESTIMATES OF PREY ABUNDANCE

A Floreana racer ingesting a juvenile marine iguana (*Amblyrhynchus cristatus*) on Gardner-by-Floreana.

Photo: Henry Herrera

4.1 ABSTRACT

Understanding the diversity and availability of food items of species of conservation concern is essential for management planning. During this project, I investigated for the first time the diet of the Floreana racer. I investigated the diversity of food items by direct examination of faecal samples collected in the field. The Floreana lava lizard (*Microlophus grayii*) and the Floreana gecko (*Phyllodactylus baueri*) were identified in 34% and 17% of the faecal samples respectively. I also conducted a pilot study on the density of Floreana lava lizards on Champion and Gardner-by-Floreana as well as a section of the Coast of Floreana Island named “Champion Bay”. Champion and Gardner-by-Floreana exhibit comparable densities of lava lizards with 176/ha and 186/ha lava lizards respectively. I did not detect enough lava lizards on Champion Bay to estimate density per area. The few lava lizards encountered (5 individuals on 16% of counts) were restricted to the rocky shore close to the waters edge. My pilot study indicates that lava lizards in Champion Bay are closer to the rocky shore, where depredation by cats and possibly rats might be lower. Although the density of a common prey item for Floreana racer falls within the recorded range of the remnant populations of the species, the presence of rats and cats remains the limiting factor for the reintroduction of the Floreana racer onto Floreana Island. Further studies are needed to better characterise the diversity of prey items year-round for this endemic racer species, in order to refine a translocation strategy.

4.2 INTRODUCTION

The conservation of a species requires a thorough understanding of a range of including threats, distribution, life history traits, genetic factors and diet (Sarkar et al., 2006). Diet studies represent an important component of conservation planning due to the critical information they provide about the nutritional requirements of species of conservation concern (Ontiveros, Pleguezuelos, & Caro, 2005). This is particularly relevant for conservation translocations since the target species is likely to encounter a different range of food items and densities in its release location compared to source locations. Starvation is a potential cause of translocation failure, due to the stress factors associated with translocations, these factors can be exacerbated by a lack of prey availability at the new site (Dickens, Delehanty, & Romero, 2010). Thus the study of diet is a vital component to the successful management of any species.

Snakes are a highly diverse group of vertebrates with regards to their morphology, behaviour and feeding ecology (see Chapter 1). Several snake species are prey-specialists while others are prey-generalists (Drummond, 1983). Snakes also exhibit different physiological feeding mechanisms, which enables them to exploit a vast array of nutritional resources. One physiological adaptation that all snakes share is a reduced metabolic rate, that is capable of fluctuation depending on the individuals needs (McCue, 2007). The implications of a reduced metabolic rate is a reduced need to feed (Secor & Diamond, 2000). This reduction in the need to feed has a number of mitigating factors. The reduction in the feeding frequency does not mean a reduction in the amount of nutrients required. As a result, many snakes can go without food for extended periods of time, an investigating into the starvation survival strategies of three snakes, the ball python (*Python regius*), ratsnakes (Elaphe obsoleta) and western diamondback rattlesnakes (*Crotalus atrox*), found that all three species are capable of surviving 168 day periods without food through a reduction in their metabolic rates. The degree to which a species reduced its metabolic rate was varied, with the pythons showing the smallest reduction of 23%, and the rattlesnakes showing the greatest reduction of 72% (McCue, 2007).

Snakes are able to go for long periods without food due to their ability to ingest large prey items without mastication (Andrade, Cruz-Neto, & Abe, 1997). The evolution of snake's jawbones has enabled them to consume prey larger than their body in circumference (Kardong, 1977). The lower jawbone in snakes exists as two separate bones connected by a band of cartilage, this cartilaginous connection allows for the extension of a snakes mouth to accommodate large prey items (Schwenk, 2000). Snakes have been observed consuming or attempting to consume prey items two or even three times their own size. This consumption of a wide arrange of prey has enabled the diversification of snakes across a large number of habitats (Greene, 1983).

An example of prey-specialist snakes are egg-eating snakes (*Dasypeltis* spp.). These snakes prey on the eggs of neighbouring species, often birds, and have a unique adaptation, which allows them to extract the rich nutrients from inside the protective eggshell (Douglas, 2000). These species have an altered vertebrae structure which acts like a saw to cut though the shell of an egg as it passes through the mouth and down the oesophagus, while the shell is crushed by forceful contractions of the axial muscle (Coleman, Rothfuss, Ota, & Kardong, 1993). Other species, such as the Neo-tropical snail eater (*Dipsas indica*), have specialized to predate on snails and slugs (Sazima, 1989). Slug and snail eating snakes have specialized physiological adaptations that allow them to ingest and absorb the required nutrients (Britt, Clark, & Bennett, 2009). Other species such as the Barbados threadsnake (*Leptotyphlops carlae*) reach an adult size of less than 10cm (Hedges, 2008; Webb, Shine, Branch, & Harlow, 2000). These snakes, due to their diminutive size are unable to predate on large organisms. Consequently they have evolved to specialise on the consumption of small invertebrates and their young (Hedges, 2008; Webb et al., 2000).

Generalist species posses no unique adaptations, either behavioural or morphological, that have allowed them to specialize on any particular type of prey. These species predate on any species that they encounter, and as such have a highly diverse array of prey types. Generalist snake species have been documented predating on fish, reptiles, birds, insects, amphibians and mammals (DeGregario et al., 2014; Merlin & Thomas, 2013). This wide array of potential prey items is a key factor in determining the geographical diversity of generalist species (Dynesius & Jansson, 2000).

As discussed in Chapter 1, there is a distinct taxonomic bias against snake studies in the literature. This extends to a greater extent to studies of snake diet. Snakes feed infrequently, often subduing and ingesting their prey before retreating to a safe area where they can digest without the risk of predation in their impaired state. This makes the study of snake feeding and diet difficult. Dietary studies on tropical snakes are rare, particularly so, on island dwelling tropical snakes (Vitt, 1983).

Due to the difficulty of studying snakes as well as the importance of dietary studies, several methods have been developed that allow for the examination of snake diets (Kephart & Arnold, 1982). Methods such as, forced regurgitation, examination of the stomach contents, extraction of faeces or captive holding (Graça Salmomão, Santos, & Puorto, 1995; Madsen & Shine, 1993). All of these methods should be considered when planning a study on the diet of snakes. Some methods are not suitable for certain species, and others are not feasible given the working conditions. Some methods are highly invasive but provide a detailed analysis of diet, while others provide a less detailed analysis but are less invasive.

There are various accounts on the diversity of prey species consumed by Galápagos terrestrial snakes. For instance, on Espanola Island, Hood lava lizards (*Microlophus delanonis*) are the main food item for Espanola racers (Altamirano, 1991). On Fernandina Island, the Western Galápagos Racer (*Pseudalsophis occidentalis*) feeds on juvenile Land Iguanas (*Conolophus subcristatus*) (Werner, 1983), juvenile Marine Iguanas (*Amblyrhynchus cristatus*) and even marine fish on tidal pools including *Dialommus fuscus, Bolinichtys longipes* and *Labrisomus dendriticus* (Merlen & Thomas, 2013). Galápagos painted locusts (*Schistocerca melanocera*) are also mentioned as prey item of Galápagos racers in general (M. H. Jackson, 1985).

Floreana racers have been observed eating juvenile Marine iguanas on Gardner-by-Floreana (H. Herrera, pers. comm.) and inspecting nests of Small Ground Finch (*Geospiza fuliginosa*), potentially looking for nestlings (Ortiz-Catedral, pers. comm.) However, no systematic study on the diet of the subspecies has been conducted to date.

In this Chapter, I present the results of a qualitative pilot study investigating the diet of the Floreana racer. I employed a palpation technique for extracting faecal samples from live snakes from the intestinal track. This method was chosen as it yields useful information while causing limited invasiveness to closely related racer species (Williams, Ross, Morton, Daltry, & Isidore, 2016) as well as satisfying the criteria of investigating diet (Hoso & Hori, 2006; Slip & Shine, 1988). I also conducted a pilot study on the density of a common prey, the Floreana lava lizard (*Microlophus grayii*) on Champion and Gardner-by-Floreana as well as a section of the Floreana Island coast named "Champion Bay". My aim was to compare the densities of a common prey species on the two known populations of Floreana racers and an accessible site in their former historical distribution as a first step towards assessing habitat quality for reintroduction of the species. After completing 24 counts on plots on Champion Bay I only detected 5 lava lizards. This number was too low to justify more visits to this area due to cost constraints, and no further sampling was completed.

4.3 METHODS

To extract faecal samples, individuals were held firmly in one hand around the mid-body, leaving the anterior portion of the snake loose. Gentle pressure was then applied to intestinal track, three quarters way down the body. Gentle pressure was applied slowly down the snake's body until the vent until faecal matter was extracted. Due to the delicate nature of this procedure, training in the field was required, and provided by J. Daltry (see also Williams et al., 2016).

Faecal samples were collected in micro-centrifuge tubes and stored in 400 μl of ethanol. Faecal samples were examined and photographed using dissection microscopes at the Invertebrate Collection Lab of the Charles Darwin Research Station in Puerto Ayora. I recorded the presence of scales, feathers, bones and other non-digested materials. These were large enough to be identified to species level in some cases but the fragmented nature of most of the material meant only a qualitative assessment could be conducted. After examination, samples were returned to plastic tubes and deposited at the Directorate of the Galápagos National Park.

In the field, I estimated the density of Floreana lava lizards by counting individuals present on variable radius plots. Every day, observers stopped every half hour during the daylight hours from 6:00 h to 12:00 h and from 14:00 h to 18:00 h, while searching for Floreana racers. The location was georefrenced with a hand held GPS (Garmin® GPSmap 62s) and the visible radius of substrate noted. Following 5 minutes of "rest", every lava lizard seen in the pre-defined radius was noted. The calculation of lava lizard density was determined as: Lava lizard density (m^2) = Number of lizards counted per 5 min / area of survey plot.

The 5-minute rest period was implemented to allow for lava lizards potentially disturbed by the observer's arrival to come out of hiding. 5-minute observation periods were considered appropriate as longer periods of 10-minute did not differ significantly in the number of lizards detected, supporting the view that the survey method is more sensible to area sampled than duration (paired t-test, mean difference 10 min – 5 min = -0.04; $t = 3.51_{d.f.\ 46}$; Pr $> t$ 0.001; n = 24).

Estimating the density of lizards in tropical islands can be difficult as they can be highly mobile and territorial, requiring long-term mark-recapture or DISTANCE sampling methods to quantify population size (Pérez-Mellado et al., 2008; Rodda & Campbell, 2002; Ruiz de Infante Anton, Rotger, Igual, & Tavecchia, 2013). Previous studies on lava lizards (*Microlophus* spp.) in Galápagos have estimated their densities via counts along transects (Altamirano, 1991; Stebbins, Lowenstein, & Cohen, 1967) however, this approach was not practical on Champion and Gardner-by-Floreana due to the absence of transects in these sites, and the dense vegetation in large areas, that would limit the implementation of a DISTANCE based survey. The method used here is a modification of field surveys for lizards in the West Indies in areas where populations of *Alsophis* snakes occur (J. Daltry, pers. comm.), thus it was deemed appropriate, however future studies should compare the performance of this method relative to others available.

4.4 RESULTS

A total of 44 faecal samples were obtained, 10 from Champion and 34 from Gardner, representing 30% of all captured and recaptured Floreana racers available for faecal sampling. Of these, 29 samples (66%) had identifiable material. This material consisted of lava lizard scales and bones, Floreana gecko skin, feathers, racer teeth, and invertebrate exoskeletons and wings. Only 29 samples with identifiable particles, 4 contained the remains of Lava Lizards, 6 contained the remains of lava lizards as well as invertebrates, 4 contained the remains of geckos, one contained the remains of both geckos and Invertebrates, 6 contained feathers and one individual had consumed both gecko and lava lizard. Fig. 4.1 shows the diversity of prey items encountered in relation to the size and weight of the Floreana racer sampled. Some examples of the faecal content examined is presented in Fig. 4.2

I completed 14 hours of sampling for lava lizards on 288 survey points.

Table 4.1 shows the densities of lava lizards on the three study areas sampled.

Table 4.1 Density of lava lizards on Champion, Gardner-by-Floreana and Champion Bay. Densities estimated by counts on points of variable radius.

Site	Number of points sampled (n)	Density m^2	Density ha
Champion	149	0.018	176.03
Gardner-by-Floreana	139	0.019	186.92

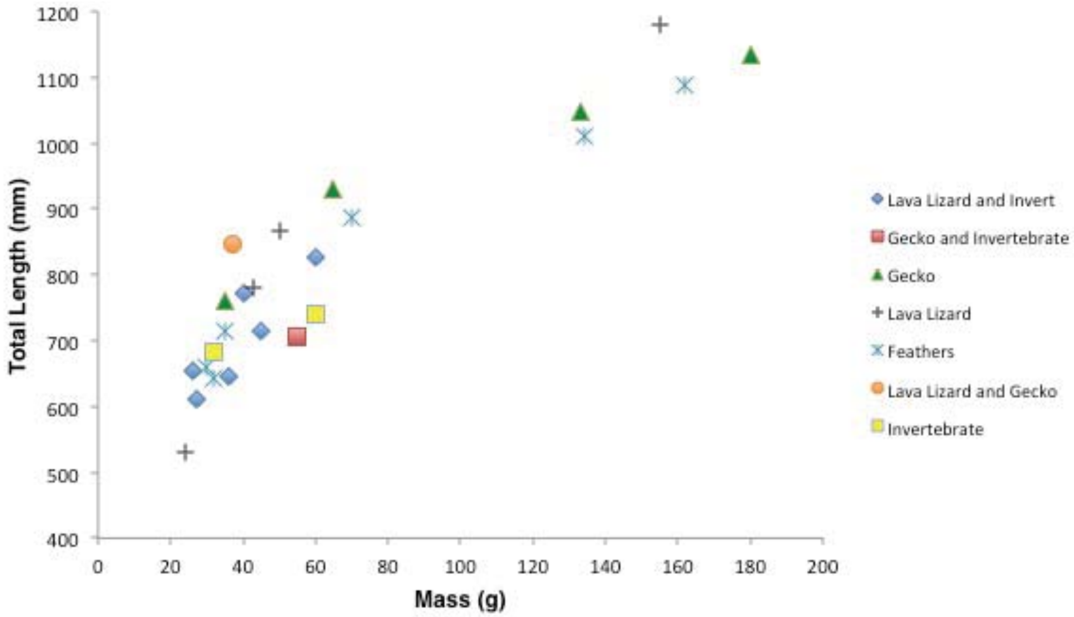

Figure 4.1 Diversity of prey items encountered in 29 Floreana racers, plotted according to the size and mass of individual snakes.

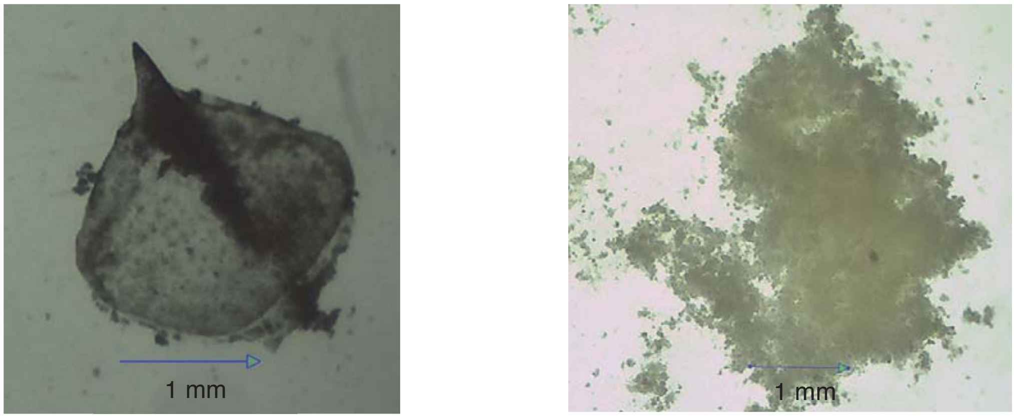

Figure 4.2 Examples of lava lizard scale (left) and gecko skin (right) found in faecal samples.

4.5 DISCUSSION

Investigating the diet of snakes in the field poses many challenges. In my study, the results do not reflect the total number of individuals captured in the field. Although I did not employ the forced regurgitation method during my study, one individual regurgitated the remains of a gecko while being transported to the processing area on Gardner-by-Floreana. The remains of the gecko were preserved as a reference to gecko scales. It also serves as a definitive confirmation that the Galápagos Racer feeds on geckos. A fact that until this observation was merely presumed, with no conclusive evidence. The evidence that the Galápagos racers feed on endemic geckos is an important development for the study of the species. As mentioned in the results section, Gardner has a density of 186.99 lava lizards per hectare and a density of 176.03 lava Lizards per hectare on Champion. However no estimates of gecko density were made during my study. The primary reason for this is the intrinsic difficulty of night work on islands and the early morning nature of snake sampling. The estimated density of lava lizards on the islets of Gardner and Champion provide a comparable measure of prey density per islet. However the unknown density of the gecko populations allows for a buffer zone.

The presence of invertebrates in the Floreana racer samples might be indicative of secondary ingestion, namely contents from the stomachs of consumed lava lizards. This has been reported (Klimstra, 1959). Secondary ingestion indicates that individuals possessed the remains of other species in their digestive tracks at the time they were consumed (J. F. Jackson, Campbell, & Campbell, 1974). This is most likely the case in this instance due to the fact that in all but two samples the remains of invertebrates were coupled with the remains of either Lava Lizards or Geckos. Many dietary analysis studies on snakes have noted the presence of invertebrate remains, and have determined that this if often the result of secondary ingestion rather than primary ingestion of invertebrate prey (Lin & Tu, 2008). However, to perform a more accurate dietary analysis, investigating the presence of feathers as well as invertebrate remains in these faecal samples, a more detailed methodology is necessary (see Chapter 5).

As part of the investigation into lava lizard density, a number of observations were made on the coast of mainland Floreana. Both point counts and single instance observations were recorded for Lava Lizards. However, only five lava lizards were detected on Champion Bay during counts. These observation confirm the presence of the species but in very low densities. Cats have been shown to alter the behavioural composition of Lava lizards in the Galápagos (Medina, Bonnaud, Vidal, & Nogales, 2014). Therefore it is highly likely that the lower density of Lava lizards on the Floreana coast is due to the presence of introduced predators.

These results, while providing novel information, have a number of limitations as a result of the methodologies. The methodologies for examining the diet of Floreana racer and the density of the Floreana Lava lizards were identified as research goals during the initial field season. The identification and rapid application of these techniques allowed for the collection of important research. However, there are a number of limitations to the data collected and it's relationship to the trends it was attempting to explain.

Faecal matter sampling has a number of limitations. It is a presence absence indicator; it can provide very little information of quantity or dietary composition (Silva & Neilson, 1985). The use of faecal analysis cannot be used to accurately determine the frequency of feeding either, due to the nature of reptile digestion being driven by temperature (Harlow, Hillman, & Hoffman, 1976), it is not possible to accurately state from the methods employed how recently the individual fed. However, the purpose of this dietary investigation was to provide a brief insight into the diet of the species and to determine the major components of the diet.

A further assumption of the model is that Lava lizards have a uniform distribution pattern across the entire study site (Holt, 1985). This is a necessary assumption of the model, due to the inability of the study to accurately cover the entire study site at once assessing all of the lava lizards present. However, it has been noted that Lava lizards are more densely clustered around sea lion colonies (Burger, 1993). Champion islet has a sea lion colony within the confines of the study site; however, the colonies on Gardner are not within the study site. This provides a contrast with regards to localized density between the study sites.

These results also have a major limitation in the application of these trends to other islands (Fielding & Bell, 1997). The purpose of this component of my research was to examine the relationship between the density of Lava lizards, as well as their patterns of activity over the course of a day, and compare these results to the encounter rates of snakes as well as the population density model. However both of these models lack data from a significant period of the day. No lava lizard surveys or snake searches were conducted between the hours of 12:00 h and 14:00 h. This was due to two factors, both related to the temperature. Temperatures in the middle period of the day were on average over 20°C due to this, the research team did not venture out from the shaded area of camp. Thus no lava lizard surveys were completed during this time. However, this is believed to still accurately represent the activity patterns of the Lava Lizards, due to the thermoregulatory needs of reptiles, and the highs in temperature during this period (Bogert, 1949). The average number of lava lizards observed per islet followed similar patterns of activity. After 11:00 h 60% of samples did not detect any lava lizards, this is mostly likely due to the thermoregulatory behaviour's (see Chapter 1) of seeking shade. It is therefore likely that if searches had been extended to include the hours between 12:00 h and 14:00 h, there would not have been a significant increase in the number of lava lizards observed.

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CHAPTER 5

CONSERVATION STATUS OF GALÁPAGOS TERRESTRIAL SNAKES AND FUTURE RESEARCH NEEDS

The author on Cape Douglas, Fernandina. In the foreground, *Pseudalsophis occidentalis* and a marine iguana.

Photo: L. Ortiz-Catedral

5.1 ABSTRACT

The terrestrial snakes of the Galápagos Islands (*Pseudalsophis* spp.) constitute an array of multiple endemic species with a problematic taxonomy and a poorly studied biology; factors which have contributed to the limited threat assessments following IUCN guidelines for this group of reptiles. This Chapter brings together the available information on the variety of threats to the conservation of these reptiles and identifies future research needs for the Galápagos terrestrial snakes in general and for the Floreana racer in particular. Most of the Galápagos racers occur across large areas with the notable exception of the Floreana racer, limited to 90 hectares of habitat on two islets off the Coast of Floreana Island. On inhabited Islands (Santa Cruz, Isabela and San Cristobal) vehicles (buses, cars and bicycles) represent a threat as regular reports of dead snakes along roads have been registered in the last 12 months. However, at this stage it is unclear the effect these have at the population level. In general, there are no negative attitudes towards endemic snakes in Galápagos, during my visits to the islands; only one report of deliberate attack on an adult snake in Santa Cruz was reported however, the opportunity exists for a pro-active public education and residents engagement in citizen science and conservation research for these poorly studied reptiles. Four priority areas of research are identified and briefly discussed.

5.2 CONSERVATION OF BIODIVERSITY

The largely human-driven biodiversity loss occurring at a global scale is an unprecedented phenomenon. The magnitude of this process is so large, that is has been labeled as “The Sixth Mass Extinction” (Barnosky et al., 2011) due to the high current extinction rate of species when compared to background rates of extinction estimated from the fossil record (Ceballos et al., 2015). Biodiversity loss however, includes more than just the extinction of species. It ranges from the erosion of genetic diversity of food crops and species extinctions, to disappearance of ecosystem-level processes (Hooper et al., 2012). These changes have a severe effect in human societies as their wealth and wellbeing rely on the services and products ecosystems provide. Thus, biodiversity loss has effects in the ecological and socio-economic dimensions.

Quantifying biodiversity loss and setting priorities for its conservation can be problematic because biodiversity encompasses genetic to ecosystem levels of biological organization (Kahilainen, Puurtinen, & Kotihao, 2014) and also because the intensity of threats and severity of biodiversity loss are distributed unevenly on the planet (Brooks et al., 2006). Thus, the possibility exists for a mismatch between the conservation outcomes of a given management action across different levels; for instance, effects at local populations *vs* effects across a species’ geographic range. For example, better-protected tiger (*Panthera tigris*) national reserves hold three to five times higher densities of this species than poorly protected reserves (Walston et al., 2014). Clearly a positive demographic outcome for tiger conservation at the local and national levels. However, despite their local importance these reserves are insufficient to maintain the genetic connectivity that would maximize the long-term survival prospects of tigers at larger geographic scales (as assessed by mitochondrial DNA) (Mondol, Bruford, & Ramakrishman, 2013; Wikramanayake et al., 2011). Thus, an integral approach to conserve tigers across their range requires local national protection and international corridors to promote and maintain genetic connectivity, not to mention management of human-wildlife conflict among other components (Wikramanayake et al., 2011). This example highlights the importance of clearly establishing the scale at which a given conservation outcome will be measured when setting up priorities to manage biodiversity loss.

Traditionally, approaches to prevent or reduce the loss of biodiversity center on the "species" as unit for theoretical analysis and/or practice. Important conservation concepts such as flagship, umbrella or keystone species have in common the use of a single species, or in some cases, suites of species to drive conservation action (D. Simberloff, 1998). Despite recent calls for incorporating a wider approach for conservation, for instance "functional diversity" (phenotypic as well as ecological distinctiveness within communities, rather than single-species approaches) (Cadotte, Carscadden, & Mirotchnick, 2011) or biodiversity hotspots (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000), "species" remain the most common unit for conservation research and management. Also, single-species programs to prevent further biodiversity loss can be complementary to ecosystem-oriented approaches (D. B. Lindenmayer et al., 2007) and can be used as units to measure conservation gains or outcomes (Gerber, 2016; Smith, Muir, Walpole, Balmford, & Leader-Williams, 2003).

5.3 THE USE OF IUCN CLASSIFICATIONS

While the use of species as the unit for establishing conservation priorities or to measure outcomes of a given program can be justified, not all species face the same probability of extinction. Consequently, classifying species into different categories of extinction risk or threat (e.g. least concern, vulnerable, critically endangered, etc.) is an active area of conservation science and seeks to assist in the prioritisation of conservation management and to highlight impacts that affect multiple species (Hoffman et al., 2008; Lamoreux et al., 2003). The international system to classify species under a range of threat categories, from “Least concern” to “Extinct” is the IUCN Red List of Threatened Species (iucnredlist.org), developed by the International Union for the Conservation of Nature (IUCN), and with contributions from scientist and wildlife managers from across the world.

Originally developed as the “Red List” or “Red Data Book” by the IUCN as loose-bound monographs (Mace & Collar, 1995; Simon, 1966), this systematic classification has been developed by the World Conservation Union, to provide information on the conservation status of a species and the various impacts (i.e. poaching, habitat loss, disease, etc.) affecting its extinction risk (Collar, 1996). These impacts can occur at various geographic levels: individual populations, across a species geographic range or even globally (Fivaz & Gonseth, 2014; Ginsburg, 2001). The combined effects of these impacts are used to classify species into different pre-defined categories of threat which include: least concern, near threatened, vulnerable, to the more serious categories of endangered, critically endangered, extinct in the wild and extinct (Rodrigues, Pilgrom, Lamoreux, Hoffman, & Brooks, 2006). The key feature that makes these categories of threat useful to identify the conservation status and needs of a given species, is these threat classifications are objective and based on data, rather than relying on subjective opinions (Proudlove, 2004).

The selection of criteria to build IUCN threat categories helps conservation practitioners to prioritise research and/or management on species and their habitats. Further, in the digital era, the IUCN Red List has become a more dynamic reservoir, undergoing regular updates, which facilitates the analysis of changes in the threat classification of a species (a proxy for species recovery) during a given time interval, or to project the effects of global phenomena on biodiversity, for instance, climate change (Akçakaya, Butchart, Mace, Stuart, & Hilton-Taylor, 2006).

Despite its pre-eminence as a conservation tool for planning and measuring the impacts of conservation actions (Rodrigues et al., 2006), the IUCN Red List has substantial information gaps. For instance, the 2012 IUCN Red List includes assessments for approximately 4% of the 1.5 million species with a formal scientific description, and there is a notable bias towards vertebrate animal groups (Hjarding, Tolley, & Burgess, 2015). Even within vertebrates, there is considerable bias towards mammals and birds, and a significant underrepresentation for other groups, such as reptiles (Squamata). A recent assessment of the extinction risk of the world's reptiles revealed that approximately one in five reptile species are classed as "Data Deficient" (Böhm et al., 2013), highlighting the lack of basic biological and demographic information for numerous species.

Conservation planning for data deficient, or unclassified species, can be challenging because it is difficult to prioritise management actions when the range of threatening processes and their relative effects at the population or species level are unknown. The IUCN thus advocates the research for "Data Deficient" species (IUCN, 2012). Ideally, such research should yield results that facilitate a classification of the target species into one of seven IUCN Red list categories (Morais et al., 2013), which are: Least concern; Near Threatened; Vulnerable; Endangered; Critically Endangered; Extinct in the Wild; or Extinct (IUCN, 2012). Further challenges for conservation planning are species with an unclear taxonomy, which can stall the assessment of a species or groups of species.

An example of a group that has a high number of described species (9084) (Uetz, 2010) but a low number of IUCN assessments are Reptiles. In 2004 only 490 species had a satisfactory IUCN threat assessment (Baillie, Hilton-Taylor, & Stuart, 2004). This situation prompted an initiative called the "Global Reptile Assessment" (GRA), which sought to correct this situation. As a result, by 2011 approximately 3200 species (nearly 35% of reptile diversity) had formal IUCN assessments (IUCN, 2011).

The Galápagos Islands (Ecuador) represent an important frontier for the IUCN assessment of island's biodiversity. Currently 624 Galápagos species have been assessed and of these 4.8% (approximately 30 species) are reptiles (iucnredlist.org). Several Galápagos reptile species remain without IUCN assessment; specific groups in particular are highly underrepresented. The majority of Galápagos Giant tortoises (*Chelonoidois*) have IUCN assessments, all species of Galápagos Iguana, both marine (*Amblyrhynchus cristatus*) and terrestrial (Genus *Conolophus*) have IUCN assessments but as of 2017 only two species of Galápagos Racer (Genus *Pseudalsophis*) have IUCN assessments (iucnredlist.org, 2017).

5.4 IUCN STATUS OF *PSEUDALSOPHIS*

The genus *Pseudalsophis* remains poorly studied, as previously mentioned in Chapter 1. This deficiency of study has translated into no IUCN assessment for the majority of the genus with the exception of three species *Pseudalsophis elegans*, *Pseudalsophis occidentalis* and *Pseudalsophis dorsalis* (Marquez, Cisneros-Heredia, & Yanez-Munoz, 2016a, 2016b; Richman & Böhm, 2011). *Pseudalsophis sleveni, Pseudalsophis steindachneri, Pseudalsophis hoodensis* and *Pseudalsophis biserialis* all remain unassessed. All of these species inhabit different islands (Table 5.1) in the Galápagos Archipelago; this results in a differentiation of localised conditions between some species, but also a number of unifying factors. Based on a preliminary examination of the species it is possible to identify a number of significant factors. Introduced species, human induced habitat change, geographic and genetic isolation and small habitat ranges are the major factors impacting *Pseudalsophis*.

Table 5.1 Galápagos terrestrial snakes and known geographic range in the Galápagos Archipelago, Ecuador.

Species	Islands
Pseudalsophis biserialis biserialis	Champion, Gardner-by-Floreana
Pseudalsophis biserialis eibli	San Cristobal
Pseudalsophis dorsalis	Santiago, Rábida, Santa Cruz, Baltra, Santa Fe
Pseudalsophis hoodensis	Española
Pseudalsophis sleveni	Fernandina, Isabela, Pinzón
Pseudalsophis occidentalis	Fernandina, Isabela, Tortuga
Pseudalsophis steindachneri	Santiago, Rábida, Santa Cruz, Baltra

The species *Pseudalsophis biserialis* is currently recognised to occupy three islands, the island of San Cristóbal and the islets of Champion and Gardner-by Floreana. A sample was first collected by Charles Darwin on Floreana Island in 1835, indicating that it was historically present on the island (Estes, Grant, & Grant, 2000). As previously discussed in Chapter 1 this species historically occurred on Floreana Island, where it is now locally extinct (Steadman, 1986).

5.5 ANTHROPOGENIC THREATS

Without a formal classification of the relevant threats that these species face, they have co-existed with anthropogenic factors since the settlement of humans in 1832. The islands of Santa Cruz, Isabela and San Cristobal all have species of snake that occur naturally, and are constantly interacting with humans. The interactions of humans on endemic species is known to have an impact on the behaviour (Stone, Snell, & Snell, 1994), population numbers and population composition of many species in the Galápagos islands as well as other island ecosystems (Li, Belasen, Pafilis, Bednekoff, & Foufopoulos, 2014; Loope, Hamann, & Stone, 1988). It is therefore reasonable to expect that there will be a greater impact on populations of Galápagos terrestrial snakes on inhabited islands.

One of the main impacts that humans have on reptilian species, especially snakes, is the development of road networks that fragment habitat and provides a significant hazard to traverse (Fahrig & Rytwinski, 2009). The Galápagos Archipelago consists of 19 major landmasses and 100 smaller landmasses; 5 of which have human structures and habitation. Santa Cruz, San Cristobal, Isabela and Floreana all have human populations and the island of Baltra has the international airport. Of these five islands with continual human disturbance, four have one or more species of snake.

The only inhabited island not to have a species of snake is Floreana Island. The species of Galápagos racer that historically inhabited Floreana is now locally extinct. The primary reason for this is thought to be the introduction of cats (Steadman, 1986). The island of Floreana was the first island settled by humans, this is the primary cause for the greater number of local species extinctions than any other island in the archipelago (Eliasson, 1982).

The four inhabited islands of Galápagos, Santa Cruz, Isabela, San Cristobal and Floreana have asphalt, and dirt roads with different degrees of vehicle traffic. In addition, the Island of Baltra has asphalt roads that connect the Airport to the pier that takes hundreds of thousands of tourists. Roads are a serious hazard to animals, as they provide barriers to movement as well as gene flow (Row, Blouin-Demers, & Weatherhead, 2007). Certain species are more susceptible than others to the impacts of roads (Forman & Alexander, 1998). Reptiles are especially vulnerable (Fahrig & Rytwinski, 2009), due to their slow locomotion and the fact that they often use road surfaces for thermoregulation (Rudolph, Burgdorf, Conner, & Schaefer, 1999). Islands with both *Pseudalsophis* species and road networks have higher degrees of fragmentation, restricted movement and risk to the populations, in comparison to islands free of roads.

5.6 INTRODUCED PREDATORS AND BROWSERS

One of the most serious threats to an ecosystem is the introduction of non-native species that can predate on, or compete with, endemic species (Clavero & García-Berthou, 2005; Gurevitch & Padilla, 2004; Lawler et al., 2002). Introduced organisms can alter the composition of an ecosystem and displace or remove native species (F. Cruz, Donlan, Campbell, & Carrion, 2005; Vitoųsek, D'Antonio, Loope, Rejmánek, & Westbrooks, 1997; Wiles, Bart, Beck, & Aguon, 2003). Some localities have much more serious threats than introduced predators, such as habitat loss, over exploitation or pollution (Venter et al., 2006; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). The severity of a threat, is entirely dependent on the specifics of the given species or ecosystem. Several major threats have been identified to global biodiversity, overexploitation, invasive species, anthropogenic effects, global climate change and disease. A study comparing the most impacting threats of China and the USA determined that introduced species are one of the least impacting threats on Chinese vertebrate species, only affecting 3%, in contrast to the United States, where 47% of species are impacted by invasives (Yiming & Wilcove, 2005).

It has been well studied in island ecosystems that the introduction of alien species can have a dire effect (K. Campbell & Donlan, 2005; Parkes, 1990; Rodda & Savidge, 2007; Daniel Simberloff, 1995), and if they are not managed quickly they can become widespread and extremely difficult to remove (Schofield, 1989). The introduction of the Brown Tree Snake (*Boiga irregularis*) to the island of Guam has resulted in the extinction of 13 of the 22 native birds that breed on the island and several species of bat and lizard (Rodda & Savidge, 2007). The introduction of this invasive species to a single island resulted in the loss of several species since its introduction after World War 2 (Engbring & Fritts, 1988; Wiles et al., 2003).

The Galápagos Archipelago has several species of invasive animals and plants, introduced by humans over 200 years ago (Restrepo et al., 2012). These species have had a documented effect on the flora and fauna of the islands and continue to do so on the islands that they inhabit (K. E. Campbell, Donlan, Cruz, & Carrion, 2004; Donlan et al., 2007; Hamann, 1979; Jäger, Kowarik, & Tye, 2009). The destructive impact of introduced species on the natural habitat has prompted several eradication programs, each targeting specific introduced species.

5.6.1 Feral Goats and Donkeys in the Galápagos

One of the most widespread introduced species in the Galápagos Archipelago is the feral goat (*Capra hircus*). This species fed on the flora, resulting in vast ranges of habitat destruction and modification (K. Campbell & Donlan, 2005; K. E. Campbell et al., 2004; Donlan et al., 2007; Hamann, 1979, 1993). The combined destruction of natural habitat by native and introduced species results in higher levels of predation on the displaced species. The destructive impact of this introduced species on the native flora of the islands has identified the feral goat for eradication (K. E. Campbell et al., 2004; Donlan et al., 2007; Guo, 2006). As a result, feral goats have since been removed from 13 Islands including Marielas, Santa Fe, Baltra, Pinta, Espanola, Marchena, Floreana, San Cristobal, Santaigo, Santa Cruz, Isabela (V. Carrion, Donlan, Campbell, Lavoie, & Cruz, 2011) but the risk of reintroduction of these browsers exists (V. Carrion et al., 2011).

Another introduced animal that acts in an identical manner to the feral goat is the feral donkey (*Equus asinus*). Feral donkeys were introduced to the Galápagos for use as pack animals. By the 1880s there were numerous donkeys roaming the islands of Isabela, San Cristobal, Santiago, Floreana and Santa Cruz (Baur, 1891). Introduced mammals were first introduced to

Floreana Island during the first human colonization of the archipelago (Restrepo et al., 2012; Steadman, 1986). Feral donkeys feed on the vegetation, in direct competition with the endemic grazers, such as the Giant Tortoise (*Chelonoidis*) and the Giant Land Iguana (Genus: *Conolophus*) (Victor Carrion, Donlan, Campbell, Lavoire, & Cruz, 2007). The feral goats and donkeys have only been removed from the archipelago in the last 40 years years (K. Campbell & Donlan, 2005; K. E. Campbell et al., 2004; Victor Carrion et al., 2007; Donlan et al., 2007), allowing the slow regeneration of vegetation, in particular *Opuntia* cactus, which are slow growing and can take 100's of years to restore (Hamann, 1979).

5.6.2 Feral Pigs on Galápagos ecosystems

One of the most impacting invasive species that has been introduced to the Galápagos Archipelago is the feral pig (*Sus scrofa* L.). The feral pig not only feeds on the native vegetation but has also been documented with remains of a Galápagos racer in its stomach contents, as well as the remains of lava lizards (Coblentz & Baber, 1987). Unlike the feral goats or donkeys, the feral pigs not only modify the habitat, they also consume endemic species. These pigs have been documented predating on the nests and hatchlings of giant tortoises (*Geochelone elephantopus*) in the Galápagos (MacFarland, Villa, & Toro, 1974) and on the nests, chicks and adults of the Galápagos Dark-Rumped petrel (*Pterodroma phaeopygia*) (J. B. Cruz & Cruz, 1987). Due to the combined nature of vegetation removal and active predation, the feral pig is a severe threat to the endemic flora and fauna of the Galápagos. The threat of feral pigs to invasive species has been identified. This species has already been successfully removed from the island of Santiago in 2000 (F. Cruz et al., 2005).

5.6.3 Feral and Domesticated Dogs and Cats in the Galápagos

Despite the fact that several species of invasive mammals have already been targeted for eradication and some have been almost completely removed from the archipelago, there are still invasive mammal species that remain and continue to adversely affect the flora and fauna. One species that continues to have an impact on members of the *Pseudalsophis* genus is feral dogs (*Canis familiaris*). Feral dogs occur alongside domesticated dogs on the islands on Isabela, Santa Cruz and San Cristobal (Barnett, 1986; Gingrich, Scorza, Clifford, Olea-Popelka, & Lappin, 2010; Jiménez-Uzcátegui, Zabala, Milstead, & Snell, 2016). Domesticated dogs are present on the island of Floreana, however, feral dogs have been removed (Barnett & Rudd, 1983).

Feral dogs have been documented pack hunting large mammals and even humans in the continental United States (Scott & Causey, 1973). In the Galápagos, feral and domestic dogs have been observed predating on Marine Iguanas (*Amblyrhynchus cristatus*) as well as adult land Iguanas (Genus *Conolophus*) (Kruuk & Snell, 1981; Phillips et al., 2011). Due to their social hunting behaviour feral dogs are formidable predators and have been recognised as a threat to endemic species (Young, Olsen, Reading, Amgalanbaatar, & Berger, 2011). No formal study has been undertaken in the Galápagos investigating the impacts of these dogs on the Galápagos Racer. It is therefore impossible to accurately estimate the impact of feral dogs on racer populations.

Similar to the feral dog is the feral cat (*Felis catus*). This species occurs alongside domesticated cats on the islands of Isabela, Floreana, San Cristobal and Santa Cruz (Dexter et al., 2004). Domesticated cats are restricted to the inhabited islands of Floreana, Isabela, San Cristobal and Santa Cruz. Feral cats were eradicated from the island of Baltra in 2004 (Phillips et al., 2011) due to their impact on hatchling Land Iguanas. Feral cats have been attributed to the extinction of many endemic species, particularly island endemics (Nogales et al., 2004).

No formal study has taken place in the Galápagos looking at the effects of cats on Galápagos racer populations. It is possible to infer from the observations of residents as well as studies on the effects of cats on other islands, the degree of impact that is occurring on the Galápagos racer. Dr Karl Campbell was present for the eradication of a feral cat on the north side of Wolf volcano in 2003. Upon examination of the stomach contents, the remains of 9 snakes were discovered (K. Campbell, per comm.). A study on the introduced cats on Isabela Island in 1987 found that their optimal periods of diurnal activity were during the morning and afternoon. During the midday hours there is less active prey, as well as greater rates of desiccation due to the higher temperatures (Konecny, 1987).

Cats are classed as one of the worst invasive species in the world and have been especially prevalent on islands (Lowe, Browne, Boudjelas, & De Poorter, 2000; Nogales et al., 2004). Cats are able to inhabit a wide range of habitats due to their highly adaptability biology. Humans have introduced feral cats to a large number of ecosystems including many islands, either intentionally or inadvertently (Coman & Brunner, 1972). In addition to the adaptable nature of feral cats to new environments there is also a documented naivety of island species when confronted with predators (Blumstein & Daniel, 2005; Cooper, Hawlena, & Pérez-Mellado, 2009; Cooper, Pyron, & Garland, 2014; Rödl, Berger, Romero, & Wikleski, 2007; Vitousek, Romero, Tarlow, Cyr, & Wikelski, 2010). These compounding effects often result in high rates of predation often resulting in the extinction of endemic species (Berger, Wikelski, Romero, Kalko, & Rödl, 2007).

Predation by cats has been the cause of extinction for a number of endemic species on islands, including reptiles (Iverson, 1978; Mitchell et al., 2002). Feral and domestic cats are widespread across the Galápagos archipelago, with only a few islands and islets remaining free of cats.

5.7 REDUCED GENETIC DIVERSITY

Loss of genetic diversity on small populations is a common topic of discussion and a regular concern for conservation biologists (O'Brien, 1994; Slatkin, 1977; Spielman, Brook, & Frankham, 2004). In the Galápagos Island, loss of haplotype diversity and heterozygosity following population decline has been confirmed for the Floreana mockingbird (*Mimus trifasciatus*) (Hoeck et al., 2010) and on some populations of Land iguanas (*Conolophus subcristatus*) (Snell, Snell, & Tracy, 1984; Tzika et al., 2008). To date no study has quantified the potential loss of genetic diversity among Galápagos terrestrial snakes, but this is a topic that warrants investigation particularly on range-restricted species such as the Floreana racer. Studies on other island racers have highlighted the risks of genetic loss in Antiguan racers (*Alsophis antiguae*) (Jennifer C. Daltry, Anthonyson, & Morton, 2010; J. C. Daltry et al., 2001; J. C. Daltry et al., 2017; Jenny C. Daltry, Morton, Smith, & Sylvester, 2003) and Saint Lucia racers (*Erytholamprus ornatus*) (Williams, Ross, Morton, Daltry, & Isidore, 2016), however to date there are no studies targeting this issue in a quantitative matter. Interestingly, a classic paper highlighting the positive impact of translocations and 'improved' genetic diversity comes from a study on populations of a snake: The Swedish Adder (*Vipera berus*) (T. Madsen, Shine, Olsson, & Witzell, 1999). Since West Indies racers have been translocated to islands of various sizes, it would be interesting to investigate the genetic makeup of source and translocated populations to quantify changes in haplotype diversity and heterozygosity. A similar studied could be devises for Galápagos terrestrial snakes where a number of species occur on islands of different sizes. For the Floreana racer, it will be a priority to investigate the degree of genetic isolation of the Champion and Gardner-by-Floreana populations to assist in the development of conservation goals with a genetic component, which represents an increasing area of investigation for Galápagos reptiles (Milinkovitvh et al., 2004; Tzika et al., 2008).

5.8 SUMMARY OF THREATS

Introduced browsers and predators represent potential risks to Galápagos terrestrial snakes, although such risk has not been quantified. This represents an opportunity for research and public engagement. Encouraging the voluntary reporting of sightings of snakes on the inhabited islands of Galápagos as well as dead specimens found on roads or killed by domestic dogs or cats, can provide information to assess the effect of these threats on snakes inhabiting in the immediate vicinity of the major towns in Galápagos: Puerto Ayora (Santa Cruz), Puerto Villamil (Isabela), and Puerto Baquerizo Moreno (San Cristobal). These approaches could be replicated on Puerto Velasco Ibarra on Floreana Island following the eradication of rats and cats and after the reintroduction of Floreana racers. As discussed in Chapter 1, the subspecies disappeared from there in the late 1800's. Because the Floreana racer exists only on Champion and Gardner-by-Floreana, maintaining these islets free of these predators is a top priority for the conservation of the Floreana racer. This can only be achieved through the synergistic approach of the Bio-security Agency of Galápagos (ABG) and Directorate of Galápagos National Park (DGNP) as well as tourism operators and scientists visiting these sites. All visitors must observe the quarantine and bio-security regulations outlined by government agencies from the Ministry of the Environment of Ecuador. The potential for reduced genetic diversity on the viability of Galápagos terrestrial snake populations also warrants examination.

5.9 FUTURE RESEARCH

As the first study on the Floreana racer, the information presented here represents novel information of a poorly studied taxon. I identify a few avenues for future research to better plan the reintroduction of the species to Floreana Island.

5.9.1 Future Dietary research

The dietary analysis component of this study was identified during fieldwork. As such the results it could provide were limited by the sampling methodology. The results provide by this analysis highlight the diverse nature of the dietary profile of the Floreana racer (detailed in Chapter 4). However, if an depth dietary analysis is identified a priority for this species due to the proposed translocation, further research will be necessary. An in-depth dietary analysis could be undertaken utilizing a number of methodologies. These methodologies were not utilized in this study due to the main focus of this research being the populating estimates and morphological description of the species. However, factors identified during this study can inform the most suitable sampling methodology.

Environmental DNA (eDNA) studies are one such method that could be utilized for an in-depth sampling of the diet of the Floreana Racer. eDNA sampling utilized the trace DNA present in the stomach contents or faecal remains to determine the species present (Taberlet, Coissac, Hajibabae, & Rieseberg, 2012). eDNA is a useful tool both in the conservation of a species as well as investigations into it’s biology (Bohmannn et al., 2014; Shokralla, Spall, Gibson, & Hajibabae, 2012). However, the use of eDNA sampling has limitations for its use as a dietary sampling tool. The major limitation of the use of eDNA in the context of studying the diet of Floreana Racers, is that each prey species, or potential prey species, requires DNA barcoding (Valentini, Pompanon, & Taberlet, 2008). It would be necessary to collect a DNA sample and generate a DNA barcode for each prey species and a number of potential prey species. While some species, such as the Floreana lava lizards (*Microlophus grayii*), have previously been sequenced, the Floreana Gecko has not (Kizirian, Trager, Donnelly, & Wright, 2004). Also from the preliminary dietary analysis as part of this study, there appears to be the remains of a number of invertebrate species (see Chapter 4 for more details). To obtain a complete eDNA sample, it would also be necessary to obtain DNA samples from a variety of invertebrate species on the islets. One further factor that requires consideration when considering eDNA is that the analysis of eDNA is a more expensive option to consider, despite the rapid decrease in DNA sequencing costs, depending of the number of samples that require sequencing, this option can still be expensive (Thomsen & Willerslev, 2015).

An alternative methodology that could be utilized to determine the diet of the Floreana Racer is the forced regurgitation of the latest prey item. The forced regurgitation methodology relies on forcing a snake to regurgitate the latest prey item for examination and then allowing the snake to re-ingest the prey item (Hirai & Matsui, 2001). This method requires the gentle palpitation of the snake to encourage it to regurgitate the most recent prey item (Gregory & Issac, 2004). However many snakes feed infrequently on larger prey items and then retreat to a safe location to digest their prey (Secor & Diamond, 2000). Therefore in the event that a handled snake is in search of food when it is encountered, it is unlikely that it will have identifiable remains present for regurgitation. A study on the foraging snakes *Thamnophis melanogaster* and *T.equesi* found that, on average, on 30% of the handled individuals regurgitated an identifiable prey item and only 2 individuals had regurgitated more than one item (Drummond & Garcia, 1989). In comparison to the faecal sample analysis utilized in this study, where samples were obtained from 35% of individuals. Despite the difficulty in accurately determining the species from which the sample originated, the use of faecal samples yielded more results than a study that employed the regurgitation method.

5.9.2 Dispersal Studies

During this study a number of individuals were recaptured a number of days after their initial capture and release. A total of 17 individuals were recaptured of the course of this study, and of those 17 individuals the distance between capture and recapture could only be determined for 10 individuals. These 10 individuals, however, displayed erratic patterns of dispersal between capture and recapture instances with an average distance of 170 m (see Chapter 3 for detail on the individual distances and number of days between captures).

These results provide a limited view of the dispersal rates of the Floreana racer, however they cannot be used as an in-depth study of dispersal. This is due to the brief glimpse that a mark-recapture provides on the movement of individuals (Keogh, Webb, & Shine, 2007). A trend observed through the mark-recapture distances is the greater the time between recaptures, the greater the distance. Three individuals were recapture over 300 days from their initial capture and all had moved over 370 m from their original capture site, and individuals that were recaptured 37 days after their initial capture and had moved and average of 27 m from their initial capture location. Other individuals however, display alternate patterns; one individual was recapture 30 days after its initial capture and had moved 69 m. Another individual was recaptured 363 days after initial capture and had was encountered 27 m from its initial capture site.

These findings illustrate the errors in the use of mark-recapture data as a pilot for the investigation of dispersal. There are no indicators of the movement of individuals between these sample points, capture and recapture. Without a dedicated study that examines the dispersal, it is impossible to determine whether the individual who appeared to have moved 27 m after 363 days, had in fact merely been recapture close to its initial capture site by chance. The use of capture-recapture locations to determine dispersal will result in an inaccurate representation of the movement of individuals due to the ‘snapshot’ results that it provides.

Despite these initial results on the movements of Floreana racers these findings are not conclusive evidence that the dispersal rates for the Floreana racer are known. The use of a dispersal-based study is useful in the context of monitoring a translocated population. If patterns of dispersal are known then it is possible to infer a sampling distance in which there is a higher encounter rate for translocated individuals (Bowman, Cappuccino, & Fahrig, 2002). This is especially useful in cryptic species such as snakes (Bickford et al., 2007). Due to the fact that very little information is known on the Floreana racer and it is currently geographically restricted, it is unwise to translocate individuals into an area where they will be exposed to a different environment without a suitable monitoring (Germano & Bishop, 2008).

5.9.3 Refinement of the prey density estimates

The prey density estimate developed as part of this study, as described in Chapter 4, is aimed a quantifying the density of the Floreana Lava lizard (*Microlophus grayii*) to determine if there is a relationship between the density of this prey species and the density of Floreana racers. This information is also of critical importance in the context of a translocation, as it provides a estimator of the necessary density of prey items required to sustain a population of Floreana Racers. However for a more informed dietary study is necessary for the effective planning of a translocation for this species. In addition to the Floreana Lava Lizard being identified as a major component of the diet of the Floreana racer, an additional species that was found in the faecal remains was the presence of the Floreana gecko (*Phyllodactylus baueri*). Gecko remains were found in 20% of the faecal samples analyzed, in comparison to 37% of samples that contained Lava Lizard remains. This indicates that geckos are an important compoentn of the diet of the Floreana racer, and as such knowledge of their numbers is crucial for a reintroduction strategy. However, no estimate of gecko density was made during this study.

Therefore, while an estimate of the density of lava lizards has been constructed as part of this study, no estimate of gecko density was made. Based on the results of the faecal sample analysis, geckos form an important part of the diet of the Floreana racer. Therefore an in-depth study of the gecko density on the islets of Champion and Gardner as well as areas of Floreana Island is a necessary pre-requisite for the planning of any translocation strategies.

5.9.4 Genetic sampling and analysis

In addition to the morphological data collected during this study a number of genetic samples were also collected from handled individuals. These samples had the intended purpose of providing material with which to develop a genetic profile for the species. However, due to unforeseen circumstances, this information was not available for the purposes of this thesis. Despite the inability of this thesis to describe the results of the genetic findings, the importance of constructing a genetic profile for this species remains paramount. Genetic profiles can shed light on a number of potential important factors, such as inbreeding depression, limited genetic variation or inherent genetic defects (Mallet, 1995) .

Genetic samples could provide insight into the phylogenetics of the snake species of the Galápagos. These species we classified by Thomas in 1997 based on their morphological features and the structure of the hemi-penis, however historical authors previously distinguished multiple species where now only one exists (Thomas, 1997; Van Denburgh, 1912). Due to the multiple taxonomic and phylogenetic reclassifications of these species by qualified experts, it is unlikely that the issues of phylogeny and taxonomy could be suitably resolved using morphological data alone.

The use of genetic data has uncovered previous thought extinct species within the Galápagos, a closely related remnant population of the Floreana Giant tortoise previously classified as extinct has recently been discovered on a different island than it's ancestral species (Hennessy, 2015).This was achieved through the use of genetic sampling techniques, to determine that a population previously undistinguished by its morphological variability. The use of genetic sampling, even in the Galápagos, has already identified new units for conservation. The use of further genetic studies, is therefore a key component of future research agendas (O'Brien, 1994). There has been a call for genetic in remote fieldwork studies, thus combining the key components of that the fieldwork aims to achieve and the collection of samples from remote species (Bunting, Burnett, Hunter, Field, & Hunter, 2014).

The use of genetic sampling on a number of species has previously resulting in the taxonomic revision of the species as well as the possible classification of new species. The South-eastern Cascade frog (*Rana livida*) has recently undergone a taxonomic revision, as well as the classification of six distinct species based on the results of a genetic sampling effort (Bain, Lathrop, Robert, Orlov, & Cuc, 2003). Genetic sampling has provided a measure of differentiation between morphologically similar species (DeSalle & Amato, 2004; DeSalle, Egan, & Siddall, 2005). Genetic samples can be utilized to resolve the taxonomic and phylogenetic classification of the Galápagos racers, they can also be used to examine differences between islands and islets (Hajibabaei, Singer, Hebert, & Hickey, 2007). The samples collected over the course of this study could shed light into the genetic differences between the two islets. As discussed in Chapter 2, there are a number of differences in morphology, which are possibly attributed to the sample sizes from each islet. However, there are enough genetic samples from each islet to construct a suitable DNA profile for each population. The construction of DNA profiles for each islet could determine whether these differences are due to the samples sizes from each islet or due to genetic differences between islets (Moritz, 1999).

5.9.5 Growth rate assessments and refinement of sampling techniques

A further between islet comparison that can be utilized in the context of a future avenue of study is an in-depth look at capture versus recapture comparisons. Certain morphological features, such as weight or length, vary temporally. These temporal variations can be examined in a mark-recapture study under the context of examining the rates of growth (Goswami, Lauretta, Madhusudan, & Karanth, 2012). Reptiles, as ectotherms, display different patterns of growth and maturation than other animal groups, such as mammals or birds (Shine & Charnov, 1992). Ectothermic species have varied rates of growth, due to their dependency on external factors. Their growth rates have also been linked to conditions faced by each individual during its juvenile life (Gotthard, 2001). However, the study of juvenile snakes is a difficult process, during this study only a small number of snakes encountered could be considered juveniles. Of the 123 individuals sampled on Champion and Gardner, only 4 could be safely assumed to be juveniles, highlighting the decreased likelihood of successfully capturing juveniles (J. C. Daltry et al., 2001).

The previous studies linking factors such as juvenile life history to the growth rates of individuals highlight the complex nature of growth in ectotherm. Therefore the morphological data obtained in this study would not be a suitable basis from which to develop a study examining the growth rates in the Floreana racer. As discussed in Chapter 2, a number of individuals appear to shrink based on a number of morphological characteristics that were measured on recaptured individuals. Due to these apparent shrinkages, research was undertaken into the possibility that a snake could shrink under conditions of starvation (Thomas Madsen & Shine, 2001). However, it has been determined that snakes don't in fact shrink but that the appearance of shrinkage in an almost inevitable conclusion of sampling length in snakes (Luiselli & Randa, 2005). This information, combined with the fact that the average change in snout vent length appears to indicate that all individuals shrunk between capture and recapture.

These factors together indicate that the length values obtained as part of this study have a degree of error associated with them. Therefore any study examining the growth rate over time on the Floreana racer would require a more accurate set of length samples. These samples would also need to be obtained on a representative sample set, as it has been discussed in previous studies that factors affecting individuals during juvenile life can impact their growth as mature individuals (Gotthard, 2001). Additionally it has been highlighted that a study attempting to examine the growth rate of a snake species also needs to take into consideration the thermal factors of the environment (Angeilletta, et al., 2004; Angilletta et al., 2002). Therefore any investigation into the growth factors of the Floreana racer will require a suitable methodology that can account for the important factors, such as an investigation into juvenile individuals, as well as accounting for the thermal factors on each islet.

5.9.6 Importance of determining the sex of snakes in future studies

One limiting factor of this study was the inability to accurately state the sex of handled individuals. As discussed in Chapter 2, the sexing of snakes relies on the examination of the hemi-penis (Pesantes, 1994). Due to a lack of expertise at examining the hemi-penis of snakes, no examinations of the hemi-penis structure were made. Without an examination of the hemi-penis structure, it was impossible to accurately state the sex of an individual. However, there is a general trend that can be measured with regards to the length of the tail relative to the total body size as well as the degree of tapering that occurs after the vent (King, 1989). A pilot study was made to determine between sexes in the field, based on the tapering of the tail after the vent. However, because I did not have an alternative method to sex individuals (i.e. molecular sexing, or examination of the genitals) the sex of individuals in the field was left unassigned. This is an important component of research into reptilian species as many reptiles, particularly snakes, display patterns of sexual dimorphism (Shine, 1994). These patterns can extend to the size of the individual (Shine, 1978), or particular aspects of their morphology, such as their head size (Camilleri & Shine, 1990). Without the ability to determine the sex of handled individuals, it is not possible to investigate these factors that are prevalent in other species. A study on the Tropical green pit viper (*Trimeresurus macrops*), found that females have a greater snout-vent length, despite males have a longer tail length relative to their total body size, females are also heavier than males and have longer and wider heads. Males also posses different patterning, with adult and sub-adult males displaying a post-ocular stripe that is not present on adult or sub-adult females (Strine et al., 2015). A common sexual dimorphism trait in snakes is female biased size dimorphism, with roughly two thirds of species displaying this pattern (Shine, 1978). However some species display alternate patterns based on their unique behavioural or physiological adaptations. Some species of snake engage in male combat to determine which individuals may mate with female, these species, due to the selective pressure for males to be larger, exhibit the inverse pattern or sexual dimorphism with males growing just as large or larger than females (Weatherhead, Barry, Brown, & Forbes, 1995). And yet other species, such as the Afro-Asian sand snake (*Psammophis schokari*), display no patterns of sexual dimorphism (Cottone & Bauer, 2009).

With snakes displaying such diverse patterns of sexual dimorphism, with both size and patterning, the study of sexual dimorphism on the Floreana racer is an important avenue of further research. By determining if there are any patterns of sexual dimorphism displayed with regard to either size or patterning, it could allow for insight into further research questions. However, before any of these avenues of further research can be identified, it is essential to determine the sex of individuals. The genetic samples, previously mentioned, have the potential to determine the sex of the individuals that have been previously sampled. However, this solution currently applies retroactively, this solution is not guaranteed for the determination of sex in future studies. Therefore it is imperative that a solution is developed to distinguish between sexes in the field. While it is possible that a pattern will emerge based on the morphological data collected and the determination of sex through genetic analysis, it is an outcome than cannot be relied upon in the planning of future studies. Therefore the most suitable solution to this issue is to examine the hemi-penis of handled individuals, due to the fact that patterns of sexual dimorphism cannot be currently relied upon to distinguish between sexes. Thomas details the hemi-penis structure of the Floreana racer in his paper (Thomas, 1997), these descriptions can be used, in conjunction with the images to determine the sex of individuals.

5.9.7 Future avenues of Ecological research

As well as the previously proposed research avenues into the species biology, there are also a number of salient points that require investigation, centering on the species ecology. Ecological studies can provide a multi-level analysis of a species and it’s role in a habitat, as well as providing insight into the ecosystem level processes that shape the biological community (D. B. Lindenmayer et al., 2007; David B. Lindenmayer et al., 2012). The understanding of these ecosystem level processes requires an understanding of the ecosystem itself, the interacting species webs, predator prey interactions, rates of mortality and fecundity. Therefore, before any ecosystem level interactions to be quantified for the Floreana racer, a number of further research avenues must be pursued to provide this basic information on the ecosystem. Without the understanding of these basic ecological processes, it is impossible to state the place of the Floreana racer within the ecosystem that satisfies the complexity of the interactions (Anderson, 2001).

This research would provide insight into the niche that the Floreana racer occupies on the islets of Champion and Gardner. While a number of aspects of this niche are known, such as the insights provided into the diet of the species, and the numbers of individuals on each islet, other aspects, such as mortality or fecundity rates, interactions with other species on the islets, or the existence of potential predators. Snakes can serves as indicators of ecosystem level processes, due to their predatory nature, they are often apex or secondary predators, thus they are sensitive to the fluctuations of the tropic levels below them (Terbough et al., 2001). The use of snakes to model ecosystem process can encounter difficulties with a lack of information regarding either the snake species or its role in the ecosystem (Beaupre & Douglas, 2009). However, very little information is known on the position of the Floreana racer in its ecosystem. Based on the preliminary diet analysis, Lava lizards and endemic geckos form an important component of the

Floreana Racer. However, very little information is known on the predators of the Floreana racer. During fieldwork on Gardner islet in 2015 a team member (J. Daltry) encountered a Galápagos Shorted eared owl (*Asio flammeus galapagoensis*) attempting to capture a Floreana Racer. A study on the owls of the Galápagos in 1983 found no evidence of snake remains present during the examination of pellets, however no collections were made on the islets of Champion or Gardner (de Groot, 1983). The islets of Champion and Gardner, as well as mainland Floreana have a different composition to the islands sampled as part of the investigation into the owls, there are no Galápagos Hawks (*Buteo galapagoensis*) present on Floreana island or it's islets. Without the natural diurnal predator, it is possible that the owls have begun to exploit a food source that was previously predated upon by the Hawks. However, this is merely conjecture, as no research has been conducted on the owls on the islets of Gardner and Champion.

A further study that is necessary on the Floreana racer, is the study of its control within the confines of its ecosystem. Species are controlled through a variety of biotic factors, such as prey availability, number of offspring produced and a number of abiotic factors, such as, the amount of available habitat or the weather patterns. A combination of these factors often regulates the number of a species and it's distribution within a given ecosystem (Naeem, 1998). On island ecosystems the available area is often the most important factor when determining the amount of a species present (Wardle, Zackrisson, Hörnberg, & Gallet, 1997). This trend could provide context as to the numbers of Floreana racer estimated to be on the islets of Champion and

Gardner. Gardner as a larger islet has a greater number of individuals. However, there are also a number of other factors that need to be considered, such as the differences in ecosystem composition and habitat. The dietary analysis of the Gardner individual's revealed the presence of possible feathers in the faecal samples, which were not present in any of the samples from Champion. This indicates a possible dietary divergence between the two islets, which could also account for the difference in population sizes. A thorough investigation into the ecosystems of the two islets could provide insight into the differences between the populations. This information could also be used in the context of a translocation to determine the appropriate the number of individuals to be moved. If there are regulating mechanisms present on the islets of Champion and Gardner that are not related to the size of the islets, such as prey availability or percentage shade cover, then any translocated individuals will still be regulated in their new ecosystem.

5.9.8 Priority areas for future research

Despite the novelty of the information provided by this research and its importance in the planned future conservation of the species, there are still a number of further avenues of research necessary. Of these avenues however, not all are of crucial importance. Of the future research avenues identified in this Chapter only one is of crucial importance, as it refines the results provided in this thesis as well as informing any future studies. The identification of sex is the most important avenue of future research as it allows for an interpretation of the data already collected, which in turn could provide insight into further research questions. The identification of male and female individuals is an important first step in the planned translocation of the species. A study on translocated tiger snakes (*Notechis scutatus*) in Australia found that translocated individuals move over a larger area than residential snakes of the same species (Butler, Malone, & Cleman, 2005). This trend indicates that translocations can affect the behaviour of snakes once translocated, indicating that any proposed monitoring strategies would need to consider this when attempting to monitor the species. One avenue of future research identified in this chapter is the need for an investigation into the dispersal of Floreana racers. The dispersal of this species would be a critical research agenda in light of a translocation to allow for an area of dispersal where translocated individuals would have a higher encounter rate. However, as noted by the study of translocated tiger snakes, translocated snakes appear to have higher rates of movement and dispersal than resident snakes, thus providing a potential problem for a dispersal study of resident snakes.

Therefore while the determination of the most appropriate method to determine the sex of individuals is the priority for future research, a further priority is the investigation of dispersal and movement before any translocation can take place. In preparation for a translocation a number of research avenues take a more urgent status, due to the necessary information they provide in the context of a translocation strategy. Research avenues such as investigating the density of geckos on both islets as well as the coast and mainland Floreana.

All of the future research avenues identified in this Chapter are important areas of research for the Floreana racer. Some, such as the determination of sex are beneficial to any further studies, while others, such as the construction of genetic profiles for the species and a genetic comparison between islets, are less essential to effectively manage the species, but no less important in furthering the understanding of the species. The choice of which research areas to pursue will be up to the individuals or team next attempting to research this species.

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APPENDIX 1

Table A1.1: Scale counts from Gardner Islet

Code	Ventral	Sub-Caudal	Supra-labials	Infra-Labials	Post-Oculars	Temporals	Head Behind Head	Mid Body	Head Before Vent
GAA	194	102	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	16	16
GAB	205	114	8(4+5)/8(4+5)	10/10	2/3	2+3+3/2+3+3	19	17	15
GAC	204	117	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+2+3	17	17	15
GAD	211	107	8(4)/8(4+5)	10/10	3/3	2+2+4/3+3+4	19	15	15
GAE	209	128	9(5+6)/8(4+5)	10/10	3/3	2+3+3/2+3+3	17	14	14
GAF	203	107	7(4+5)/8(4+5)	10/10	1/1	2+3+3/2+3+4	17	15	15
GAG	209	105	8(4+5)/8(4+5)	10/11	2/2	3+4+3/3+3+3	19	16	15
GAH	197	93	8(4+5)/8(4+5)	10/10	2/2	3+3+3/3+3+3	19	15	15
GAI	203	121	8(4+5)/8(4+5)	10/10	1/1	2+2+3/2+2+3	17	17	15
GAJ	204	123	8(4+5)/8(4+5)	11/10	3/3	2+2+3/2+2+3	19	17	15
GAK	215	111	8(4+5)/8(4+5)	10/10	2/2	2+3+4/2+2+3	17	17	13
GAL	205	105	8(4+5)/8(4+5)	10/11	2/3	2+2+3/2+2+3	20	17	15
GAM	205	118	8(4+5)/8(4+5)	10/10	2/3	1+2+3/1+2+3	19	15	15
GAN	230	116	9(4+5)/8(4+5)	10/10	2/2	3+4+3/3+4+3	19	18	15
GAO	203	121	8(4+5)/8(4+5)	10/10	2/2	1+2+3/2+2+3	19	18	15
GAP	228	116	8(4+5)/8(4+5)	10/10	2/2	3+3+3/1+3+3	18	15	15
GAQ	203	117	8(4+5)/8(4+5)	10/10	2/2	1+2+2/2+2+3	20	15	15
GAR	204	122	8(4+5)/9(5+6)	10/10	2/2	2+2+3/2+2+3	17	17	15
GAS	204	107	8(4+5)/8(4+5)	11/11	3/3	2+2+3/2+2+3	19	15	15
GAT	201	82	8(4+5)/8(4+5)	10/10	3/3	2+2+2/3+2+3	19	17	15
GAU	202	129	8(4+5)/8(4+5)	10/10	3/3	2+3+3/3+3+3	17	18	15
GAV	208	112	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	15

GAW	204	115	8(4+5)/8(4)	10/10	3/3	2+2+3/2+2+4	19	17	16
GAX	203	125	8(4+5)/8(4+5)	10/9	3/3	3+3+3/3+3+3	16	19	14
GAY	209	98	8(4+5)/8(4+5)	9/9	2/2	2+2+3/2+2+3	17	15	14
GAZ	202	106	8(4+5)/8(4+5)	9/9	3/3	2+2+3/2+3+3	19	19	15
GBA	204	96	8(4+5)/8(4+5)	11/10	2/2	2+2+3/2+2+3	19	19	15
GBB	205	107	8(4+5)/8(4+5)	9/9	3/3	2+2+3/2+2+3	19	19	15
GBC	206	112	8(4+5)/8(4+5)	9/9	3/3	2+2+3/2+3+3	19	19	16
GBD	210	95	8(4)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	15
GBE	214	116	8(4+5)/8(4+5)	8/9	3/3	1+2+3/2+2+3	19	15	15
GBF	214	112	8(4)/8(4)	10/10	3/3	2+2+3/2+2+4	19	17	16
GBG	208	114	8(4+5)/8(4+5)	8/9	3/3	2+2+3/2+2+3	19	15	15
GBH	210	116	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+3+3	19	19	15
GBI	203	117	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+2+3	17	15	15
GBJ	210	108	8(4)/9(4)	10/11	3/3	3+3+2/3+3+3	19	17	17
GBK	208	113	8(4+5)/8(4+5)	11/11	4/3	2+3+3/3+3+3	18	17	17
GBL	215	114	8(4+5)/8(4+5)	9/9	3/3	2+2+3/2+2+3	19	19	15
GBM	203	123	8(4+5)/8(4+5)	10/10	3/3	2+3+3/2+3+4	19	17	15
GBN	204	108	8(4+5)/8(4+5)	10/10	2/2	2+3+3/2+3+3	19	17	15
GBO	205	120	8(4+5)/8(4+5)	9/9	3/3	2+2+2/2+2+2	19	19	15
GBP	203	108	8(4+5)/8(4+5)	9/9	3/3	2+3+3/2+3+3	18	19	16
GBQ	204	120	8(4+5)/8(4+5)	10/10	3/3	2+2+3/1+2+3	20	16	16
GBR	203	119	8(4+5)/8(4+5)	9/8	3/3	2+2+3/2+2+3	19	19	15
GBS	203	120	8(4+5)/8(4+5)	11/10	2/2	2+3+3/1+3+3	17	19	15
GBT	204	121	8(4+5)/8(4+5)	9/10	3/3	2+3+2/2+2+3	19	15	15
GBU	210	111	8(4+5)/8(4+5)	9/9	2/2	2+2+3/3+3+3	19	15	15
GBV	218	95	8(4+5)/8(4+5)	11/10	2/2	2+2+3/2+2+3	19	17	15
GBW	209	108	8(4+5)/8(4+5)	10/10	3/3	2+3+4/3+3+4	17	17	15
GBX	202	122	8(4+5)/9(4+5)	9/9	3/3	2+2+3/2+3+3	19	15	15

GBY	206	108	9(4+5)/9(4+5)	9/9	3/2	2+2+3/2+2+2	19	19	15
GBZ	203	111	8(4+5)/8(4+5)	10/10	1/1	2+3+4/2+2+3	19	17	15
GCA	203	118	9(4+6)/9(4+6)	10/10	2/2	2+2+3/2+3+3	19	19	15
GCB	206	108	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+3+3	19	17	15
GCC	206	118	8(4+5)/8(4+5)	10/9	2/2	2+2+3/2+2+3	18	16	17
GCD	210	103	8(4+5)/8(4+5)	10/10	2/2	2+3+3/2+2+3	19	19	17
GCE	205	103	8(4+5)/8(4+5)	11/9	1/1	1+2+3/1+2+3	19	19	15
GCF	231	111	8(4+5)/8(4+5)	11/11	2/2	2+3+3/2+3+3	18	17	16
GCG	205	110	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	18	16	16
GCH	203	107	8(4+5)/8(4)	9/9	1/1	2+2+2/2+2+2	18	16	16
GCI	206	109	8(4+5)/8(4+5)	9/9	1/1	2+2+2/2+2+2	18	16	17
GCJ	203	110	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	18	15	16
GCK	203	110	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+3+3	19	15	15
GCL	207	112	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	17	15
GCM	206	112	8(4+5)/8(4)	10/10	1/1	3+2+3/3+2+3	19	15	15
GCN	209	111	8(4+5)/8(4+5)	11/11	2/2	2+2+3/2+3+3	15	17	14
GCO	206	107	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	17	16
GCP	210	110	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	19	16
GCQ	211	101	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+3+3	16	16	15
GCR	207	114	8(4+5)/8(4+5)	9/9	1/1	2+2+2/2+2+2	18	16	15
GCS	208	116	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	16	18	16
GCT	208	118	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	18	16	15
GCU	206	112	8(4+5)/8(4+5)	9/10	1/1	2+2+2/2+2+2	18	18	15
GCV	209	122	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	16	15
GCW	212	111	8(4+5)/8(4+5)	9/10	1/1	2+2+3/2+2+3	18	18	18
GCX	214	99	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	17	16
GCY	203	117	8(4+5)/8(4+5)	9/10	2/2	1+2+2/2+2+3	19	17	15
GCZ	209	117	8(4+5)/8(4+5)	9/10	1/1	2+2+3/2+2+3	18	19	17

GDA	213	109	8(4+5)/8(4+5)	10/10	3/3	2+3+3/2+3+3	18	18	17
GDB	201	114	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+2+3	18	18	17
GDC	203	111	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	17	16
GDD	209	111	8(4+5)/8(4+5)	9/9	1/1	2+2+3/2+2+3	19	18	15
GDE	207	108	8(4+5)/8(4+5)	9/10	2/2	2+2+3/2+2+3	17	19	15
GDF	204	116	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	17	15
GDG	211	101	8(4+5)/8(4+5)	10/10	3/3	2+2+3/3+3+2	18	19	15
GDH	197	120	9(5+6)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	15
GDI	203	120	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	17	16
GDJ	206	131	8(4+5)/8(4+5)	10/10	3/3	2+2+2/2+2+2	19	17	15
GDK	203	122	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	18	15
GDL	199	117	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	17	15
GDM	207	118	8(4+5)/8(4+5)	10/10	3/3	1+2+3/2+2+3	19	18	15
GDN	209	102	8(4+5)/8(4+5)	10/10	3/3	2+2+2/2+2+3	19	15	15
GDO	214	111	8(4+5)/8(4+5)	10/10	3/3	1+2+2/2+2+3	19	18	15
GDP	208	116	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+2	19	18	15
GDQ	206	116	8(4+5)/8(4+5)	10/10	3/3	2+3+3/2+2+3	19	18	15
GDR	211	112	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	15
GDS	203	116	8(4+5)/8(4+5)	10/10	3/2	1+2+3/2+2+2	18	19	16
GDT	211	105	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+3+3	19	19	15
GDU	204	116	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+3+3	19	16	15
GDV	208	113	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	18	18	16
GDW	206	118	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	18	15
GDX	200	67	8(4+5)/8(4+5)	10/10	3/3	2+2+3/1+2+3	18	19	16
GDY	216	126	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	18	15

Table A1.2: Scale counts for Champion Islet

Code	Ventral	Sub-Caudal	Supra-labials	Infra-Labials	Post-Oculars	Temporals	Head Behind Head	Mid Body	Head Before Vent
CAA	199	103	9(4+5)/8(4+5)	10/10	2/2	2+2+3/1+2+3	17	18	15
CAB	201	110	8(4+5)/8(4+5)	10/10	2/2	1+2+3/1+2+3	17	19	15
CAC	206	107	8(4+5)/8(4+5)	10/10	2/2	1+2+3/1+2+4	19	17	15
CAD	212	94	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	17	19	15
CAE	204	107	8(4+5)/8(4+5)	11/10	2/2	2+2+3/1+2+3	17	17	15
CAF	206	106	8(4+5)/8(4+5)	10/10	3/3	2+2+2/2+2+3	16	17	15
CAG	207	103	8(4+5)/8(4+5)	10/10	3/3	3+2+2/3+2+3	17	19	15
CAH	206	101	8(4+5)/8(4+5)	10/10	3/3	2+3+3/2+2+3	17	19	15
CAI	201	110	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	17	15	15
CAJ	206	103	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+2+3	17	19	15
CAK	203	110	8(4+5)/8(4+5)	10/10	2/2	2+2+3/2+2+3	17	17	16
CAL	208	132	8(4+5)/8(4+5)	9/9	3/3	2+2+3/2+2+3	16	18	16
CAM	200	110	8(4+5)/8(4+5)	10/9	1/1	2+2+3/2+2+3	15	19	15
CAN	206	110	8(4+5)/6(4+5)	9/9	2/2	2+2+3/2+2+3	15	17	15
CAO	208	97	8(4+5)/8(4+5)	10/10	3/3	2+3+3/2+3+3	19	19	18
CAP	213	127	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+3+3	19	18	15
CAQ	208	116	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	16
CAR	209	103	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	18	15
CAS	206	122	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+3+2	19	18	16
CAT	199	110	8(4+5)/8(4+5)	10/10	3/3	2+2+3/2+2+3	19	19	16

Table A1.3: Morphological data of Gardner Individuals

Code	Snout-Vent Length (mm)	Tail Length (mm)	Total length (mm)	Head Length (mm)	Head Width (mm)	Mass (g)	Girth (cm)
GAA	360	147	507	10.4	6.5	20	
GAB	564	227	791	16.1	9.1	45	
GAC	514	235	749	17.9	10.9	45	
GAD	634	245	879	17.8	12.4	85	
GAE	920	370	1290	22.8	15.9	195	
GAF	600	202	802	18.1	10.6	45	
GAG	596	215	811	17.4	9.7	45	
GAH	967	294	1261	25.5	19.3	195	
GAI	515	202	717	15.7	9.9	45	
GAJ	505	210	715	15.2	9.4	35	
GAK	875	366	1241	25.2	15.6	165	
GAL	884	296	1180	25.0	15.4	155	
GAM	535	240	775	15.3	8.7	33	
GAN	676	237	913	20.1	13.9	75	
GAO	605	241	846	18.0	10.1	37	
GAP	525	214	739	18.7	12.3	60	
GAQ	574	253	827	22.0	12.2	60	
GAR	450	209	659	16.1	9.6	41	
GAS	815	318	1133	23.7	15.4	180	
GAT	720	220	940	23.3	14.3	150	
GAU	546	235	781	19.2	11.3	50	
GAV	555	208	763	17.6	10.2	139	
GAW	529	220	749	16.6	9.2		
GAX	449	195	644	16.2	9.5	32	

GAY	459	162	621	16.5	8.2	33
GAZ	710	300	1010	22.8	14.0	136
GBA	508	185	693	18.5	10.3	55
GBB	570	180	750	16.8	10.2	34
GBC	695	315	1010	21.8	14.2	134
GBD	800	243	1043	23.7	15.1	184
GBE	740	307	1047	23.5	15.0	133
GBF	651	235	886	20.9	12.0	70
GBG	575	222	797	21.3	12.0	36
GBH	458	217	675	16.6	10.0	29
GBI	519	117	636	19.6	11.3	59
GBJ	675	256	931	21.4	12.0	65
GBK	632	236	868	20.2	11.5	50
GBL	435	210	645	14.7	8.8	36
GBM	620	274	894	18.9	10.6	47
GBN	545	235	780	19.0	11.2	43
GBO	480	233	713	12.6	9.1	45
GBP	433	175	608	14.1	7.5	24
GBQ	353	142	495	11.2	6.2	7
GBR	450	205	655	14.3	8.7	41
GBS	470	190	660	15.5	9.1	30
GBT	766	322	1088	13.9	22.7	162
GBU	480	191	671	9.5	12.6	36
GBV	746	215	961	25.9	17.1	185
GBW	577	220	797	18.5	10.8	53
GBX	554	219	773	17.5	9.6	40
GBY	433	179	612	15.4	7.8	27
GBZ	510	200	710	16.0	9.4	33

GCA	482	202	684	13.9	9.0	32	
GCB	500	184	684	14.9	9.1	26	
GCC	458	209	667	18.5	8.0	40	
GCD	445	190	635	17.5	11.0	28	
GCE	384	153	537	15.5	9.0	53.7	
GCF	490	170	660	17.0	9.5	66	
GCG	500	205	705	20.2	11.6	70.5	
GCH	606	204	810	21.4	11.2	50	3.9
GCI	460	183	643	17.0	8.2	64.3	3.3
GCJ	660	233	893	24.0	14.0	102	
GCK	681	290	971	22.0	15.0	133	6.4
GCL	595	265	860	23.0	13.0	86	5
GCM	535	215	750	18.6	10.3	75	4.5
GCN	453	177	630	15.1	9.0	26	3.4
GCO	661	283	944	23.4	14.0	99	5.1
GCP	555	218	773	19.2	10.0	54	4.8
GCQ	795	295	1090	25.2	16.6	164	6.5
GCR	460	185	645	15	8.2	37	
GCS	575	220	795	19.3	11.4	40	4
GCT	535	223	758	20	10.4	45	4.4
GCU	766	320	1086	15	25.3	150	5.8
GCV	798	335	1133	23.1	13.4	134	5.8
GCW	424	167	591	18	8.5	26	3.3
GCX	520	230	750	23.4	12.6	128	5.6
GCY	393	137	530	13.5	7.0	25	3.8
GCZ	500	235	735	19.2	10.0	38	3.7
GDA	495	215	710	17.5	9.8	33	3.9
GDB	542	252	794	21	12.9	75	

GDC	500	216	716	15.6	10.6	50	4.2
GDD	395	163	558	12.4	7.2	16	2.7
GDE	484	192	676	18	10.0	41	4.5
GDF	775	347	1122	24.2	16.2	181	6.6
GDG	863	301	1164	24.9	18.0	225	6.7
GDH	797	337	1134	24.2	11.6	174	5.9
GDI	431	204	635	14.4	7.5	29	3.3
GDJ	347	215	562	14.1	8.0	30	3.2
GDK	452	207	659	15	8.0	25	3.4
GDL	460	207	667	13.3	7.9	25	3.6
GDM	422	182	604	15	8.0	30	2.4
GDN	750	250	1000	21	13.0	126	5.4
GDO	798	310	1108	24	11.0	179	6.4
GDP	475	212	687	13.6	8.2	36	3.3
GDQ	577	235	812	18	10.0	34	3.2
GDR	688	269	957	20	12.8	90	4.1
GDS	537	267	804	20	11.0	56	4
GDT	559	222	781	18.2	11.3	50	3.7
GDU	785	345	1130	27.8	16.4	166	5.3
GDV	538	219	757	17	9.0	34	3.8
GDW	550	255	805	18.2	10.0	50	3.8
GDX	575	150	725	18.1	10.0	50	4.1
GDY	690	290	980	21.6	13.0	74	3.6

Table A1.4: Morphological Data of Champion Individuals

Code	Snout-Vent Length (mm)	Tail Length (mm)	Total length (mm)	Head Length (mm)	Head Width (mm)	Mass (g)	Girth (cm)
CAA	603	234	837	17.6	10.9	45	
CAB	465	175	640	14.5	8.4	15	
CAC	585	205	790	16.5	9.5	40	
CAD	527	181	708	17.1	9.0	25	
CAE	435	152	587	15.4	9.0	35	
CAF	525	180	705	15.6	8.5	55	
CAG	373	158	531	8.3	14.5	24	
CAH	480	175	655	8.5	17.6	26	
CAI	536	225	761	8.2	17.1	35	
CAJ	370	137	507	7.0	10.2	10.5	
CAK	652	287	939	13.7	27.2	158	
CAL	457	205	662	7.2	17.4	66.2	
CAM	428	205	633	8.0	15.0	63.3	
CAN	573	222	795	11.2	23.0	79.5	
CAO	387	138	525	13.5	8.9	16	2.3
CAP	483	231	714	14.6	9.0	26	2.8
CAQ	225	80	305	9	5.2	4	1.4
CAR	805	255	1060	24.2	16.0	240	6.8
CAS	485	155	640	15.6	8.1	26	2.6
CAT	447	195	642	15.8	8.2	30	3.8