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POPULATION DYNAMICS AND BEHAVIOURAL ECOLOGY OF TWO ISOLATED POPULATIONS OF THE FLOREANA MOCKINGBIRD: LAYING THE BASIS FOR ITS REINTRODUCTION

A thesis presented in partial fulfilment of the requirements for the
degree of Doctor of Philosophy in Conservation Biology at
Massey University, Auckland, New Zealand

Enzo M. R. Reyes

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In scientia, deos omnes peribunt

Floreana mockingbird, *Mimus trifasciatus*.

From Charles Darwin, *The Zoology of the Voyage of H.M.S. Beagle*.

ABSTRACT

Translocations are one of the most important conservation actions in the recovery of endangered species, these imply the movement of live individuals from one area to another. To ensure the success of translocations, different logistics and species-specific ecological factors need to be considered. Since the early 2000's, there have been calls to reintroduce the endangered cooperative breeding Floreana mockingbird, to Floreana Island (Galápagos Archipelago) where they became locally extinct due to habitat loss and invasive species. The species currently inhabiting two small islets off the coast of Floreana with no recent history of connection between populations. However, our understanding of reintroduction strategies for the mockingbird is based on monogamous breeding species, not on cooperative breeding species. In this thesis, I explored demographic and behavioural aspects of the species that might facilitate the reintroduction to Floreana. Firstly, I described a non-invasive method that will help will the correct sexing identification and monitoring of Floreana mockingbirds. Furthermore, I assessed the probability of survival of the species using capture-mark-recapture (CMR) models and the influence of precipitation on the survival rate, recruitment of individuals, and population growth. Overall, the population seem to be stable with a slight decrease in one of the populations. Additionally, I explored ecological factors such as vocalization and sociality. I investigated the hypothesis of possible differences in vocalisations between individuals from the two remnant populations. I found an acoustic divergence between populations that could be explained by the influence of cultural drift and morphological differentiation as an effect of isolation, lack of gene flow, and cultural exchange. Finally, I investigated the social structure of the Floreana mockingbird and the probability of group disruption during translocations. I found that mockingbirds live in a highly transitive hierarchy and that the dominance networks are explained by the age and social status of the individuals. Moreover, the network simulations showed that inadequate harvesting could increase the probability of group disruption in the new area of translocations. My research will help develop a reintroduction strategy for the species to Floreana Island and it will assist the Galápagos National Park to reach a major conservation milestone for the species.

RESUMEN (SPANISH)

Las translocaciones son una de las herramientas más importantes en conservación para la recuperación de especies en peligro, y consisten en el movimiento de individuos vivos de un lugar a otro. Para asegurar el éxito de las translocaciones, diferentes factores de logística y ecológicos específicos de las especies necesitan ser considerados. Desde principios del 2000, ha habido llamados para la reintroducción del Cucuve de Floreana una especie de cría cooperativa en peligro de extinción a la isla Floreana, donde se extinguió debido a la pérdida de hábitat y especies invasoras. La especie actualmente habita dos pequeños islotes en las costas de Floreana con ninguna conexión entre poblaciones. Sin embargo, el conocimiento sobre las estrategias de reintroducción para el Cucuve ha sido basados en especies monógamas y no en especies de cría cooperativa. En esta tesis, yo exploro la demografía y aspectos de comportamiento de la especie que podrían facilitar la reintroducción a Floreana. En primer lugar, yo describo un método no invasivo que ayudará con la identificación correcta del sexo y facilitará del monitoreo. Además, evalué la probabilidad de sobrevivencia de la especie usando modelos de captura-marca-recaptura (CMR) y la influencia de la precipitación en la tasa de sobrevivencia, reclutamiento de individuos y crecimiento poblacional. En general, las poblaciones parecen estar estables con un ligero decrecimiento en una de las poblaciones. Adicionalmente, exploré factores ecológicos tales como la vocalización y estructura social. Investigué las hipótesis de posibles diferencias en vocalizaciones entre las poblaciones. Encontré una divergencia acústica entre poblaciones, la cual puede ser explicada como la influencia de deriva cultural y diferenciación morfológica como un efecto de aislamiento, ausencia de flujo genético e intercambio cultural. Finalmente, investigué la estructura social del Cucuve de Floreana y las probabilidades de ruptura de grupos durante escenarios de reintroducción. Encontré que los Cucuves de Floreana viven en una sociedad altamente jerárquica y que las redes de interacción son explicadas por la edad y el estatus social de los individuos. Además, las simulaciones de las redes de interacción mostraron que un inadecuado movimiento de individuos puede incrementar la probabilidad de ruptura grupal en las nuevas áreas de translocación. Mi investigación ayudará a desarrollar una estrategia de reintroducción para la especie a la isla Floreana y asistirá al Parque Nacional Galápagos a alcanzar un importante hito de conservación para la especie.

DECLARATION

I declare that this thesis is an accurate and original account of my research and that the contents have not previously been submitted for a degree at Massey University, nor any other tertiary institution in New Zealand or overseas. Except where acknowledged, the material contained in this thesis has not been written or published by any other individual and to the extent of my knowledge, does not infringe copyright restrictions. The research presented here is part of a larger research project monitoring the Floreana mockingbird (*Mimus trifasciatus)* since 2006 by my supervisor Dr Luis Ortiz-Catedral in conjunction with the Directorate Galápagos National Park and Island Conservation. Dr Luis 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 under permit PC-74-17 and PC-08-19, see Appendix 5. Dr Ortiz-Catedral and I coordinated all the logistical support necessary to complete this investigation and 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. Financial support for the project was obtained from the Galápagos Conservation Trust, Massey University, The Rufford Foundation, and the Friends of Galápagos New Zealand Society. 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.

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Appendices

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 1

Introduction

The Galápagos mockingbirds.

Auckland, November 2020.

Enzo M.R. Reyes

1.1 INTRODUCTION

1.1.1 LOSS OF ISLAND BIODIVERSITY

The world's biodiversity is experiencing what scientists call the sixth mass extinction of the planet (Barnosky *et al.*, 2011). At present, the rate of species loss has been estimated to be over 100 times above the estimated normal rate since the beginning of the Anthropocene (Pimm, Russell, Gittleman, & Brooks, 1995). The extinction rate of vertebrates since 1560 is 60 times the magnitude observed in the most recent mass extinction (Cretaceous) 65 MY ago, with 31.6% of amphibians, 13.7% of birds, 5.2% of mammals, 18.4% of reptiles and 47.2% of fish species disappearing sometime after 1560 (McCallum, 2015). Around half of the species once present on the planet have already disappeared, together with millions of populations, with the tropics being extinction hotspots (Ceballos, Ehrlich, & Dirzo, 2017). A recent assessment concluded that at least 515 species of terrestrial vertebrates are at risk, of which 53% of them live on islands, mainly in South America and Oceania (Ceballos, Ehrlich, & Raven, 2020).

Currently, 36% of species classified by the IUCN Red List as critically endangered and endangered occur on islands (Tershy, Shen, Newton, Holmes, & Croll, 2015). During the last centuries, 273 vertebrate populations have disappeared from several islands, of which Guam has been the most affected with a loss of eight vertebrate species (Spatz *et al.*, 2017). It is estimated that 90% of bird extinctions in the last 400 years have occurred on islands, the majority on the Pacific Islands after human colonization (Duncan, Boyer, & Blackburn, 2013; Johnson & Stattersfield, 1990). The intentional or accidental introduction of exotic species, which have subsequently become invasive, has been one of the main causes of island extinctions (Szabo, Garnett, Khwaja, & Butchart, 2012). Biodiversity loss alters the balance on island ecosystems, affecting mutualist associations between animal-plant species, causing in most of the cases a cascade effect of extinctions and collapsing of the ecosystems (Heinen, van Loon, Kissling, & Hansen, 2018).

Predation by introduced species has been reported as the main extinction threat for island species (Bolam *et al.*, 2020; Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016; Dueñas *et al.*, 2018). Spatz *et al.* (2017) found that invasive species are widespread across the world's islands, present in 97% (753) of the islands assessed, with 3361 populations of 175 invasive species. For example, the impact of introduced cats (*Felis catus*) has been recorded for more than 120 islands, affecting 175 native species, of which most are threatened birds (Medina *et al.*, 2011). In the case of birds specifically, island avifauna has often evolved in isolation without the presence of significant non-avian predators and the species have either lost appropriate responses to predators or developed specific adaptations to island ecosystems that make them vulnerable to introduced predators (Roots, 2006; Steadman, 2006). Endemic flightless or ground-nesting birds are particularly vulnerable to predators such as cats, (Woinarski *et al.*, 2017) which occurr in high densities and have very flexible hunting strategies (Hamer, Gardiner, Proft, Johnson, & Jones, 2021). However, invasive species are not the only factors responsible for biodiversity loss on islands. Other reasons for the current rates of extinction in these isolated environments are synergetic process between loss of habitat, depletion of food supplies and pathogens (Brook, Sodhi, & Bradshaw, 2008; Milberg & Tyrberg, 1993).

1.1.2 ENDANGERED BIRDS ON ISLANDS AND CONSERVATION

In addition to the well-documented impact of human-related biodiversity loss, island avifauna is subject to several non-human environmental factors that can exacerbate a species' susceptibility to extinction. The majority of birds on islands are specialists and live in a restricted range (endemism). Small distribution range is usually a good predictor of extinction risk, particularly for birds (Harris & Pimm, 2008), and the habitat range size of insular bird species is significantly smaller that of continental species (Manne, Brooks, & Pimm, 1999). For example, Clavero *et al.*, (2009) in a study using gradients of variation of extinctions drivers found that island birds with small ranges are severely affected by introduced species. Additionally, ecological adaptations to island environments, such as the lack of antipredator response, flightlessness, limited dispersal, and problems associated with the "small population paradigm" (Caughley, 1994); as small populations with low genetic diversity are among other factors that influence the loss of native species on islands (Carthey & Banks, 2014; Kirchman, 2009; O'Grady *et al.*, 2006; Ricklefs & Bermingham, 2004; Spielman, Brook, & Frankham, 2004).

Of the world's 10.000 bird species, around 1750 species are restricted to islands. Of those over 400 species are categorized as threatened and the majority of these are endemic to a single island (Johnson & Stattersfield, 1990). Of 279 ultra-taxa (species and subspecies level) 78.7% of species and 63.0% of bird subspecies extinctions occur on oceanic islands compared to 9.9% and 23.2% of species and subspecies extinctions on continents (Szabo *et al.*, 2012). However, during the period 1994 to 2004, ten bird species restricted to islands were saved from extinction (Butchart, Stattersfield, & Collar, 2006) and another 18 bird species were brought back from the brink of extinction in the last decade (2010 – 2020) due to implementation of conservation actions such as the eradication and control of invasive species (Bolam *et al.*, 2020). For island species, some of the main conservation actions implemented include protection of habitats, assisted colonization, translocation, habitat restoration and the removal or eradication of invasive species (Veitch, Clout, & Towns, 2011).

1.1.2.1 Eradications

Eradication is the complete and permanent removal of an alien species in a defined area (Genovesi, 2008). Eradication of invasive species has been performed from the scale of small islands as the case of the Maria Island (1ha) in New Zealand (Towns & Broome, 2003) to large scale eradications such as Santiago Island in the Galápagos (40 000 ha) (Cruz, Carrion, Campbell, Lavoie, & Donlan, 2009; Cruz, Donlan, Campbell, & Carrion, 2005). Example of a successful large scale eradication is Dirk Hartog Island, Australia with 62 000 ha being the largest cat eradication in the world (Algar *et al.*, 2020). By 2009, there had been hundreds of eradication attempts of several mammals and bird species across the globe, most of them successful (Keitt *et al.*, 2011). Although most eradications have been undertaken on islands due to their limited size and closed system (Butchart *et al.*, 2006), there have also been a few cases of eradications at the continental scale. For instance, the successful eradication of the screwworm (*Cochliomyia* spp.) in Central America (Galvin & Wyss, 1996). Nevertheless, the outcomes of most eradications are difficult to quantify in terms of failure and success because of the presence of multiple factors in the process (financial and logistic), and because the outcomes are seldom reported in the scientific literature (Courchamp, Chapuis, & Pascal, 2003).

Despite the success of eradications in the recovery of native populations, there are some cases when eradication has had a negative impact (often short term) on the target population, usually associated with the eradication methods, secondary poisoning of non-target species is the most common. In New Zealand alone, the mortality of non-target birds by secondary poisoning has been reported in more than 10 species (Hoare & Hare, 2006). Another indirect negative effect of eradication is that the process itself could benefit other invasive species. An example of this is the increase of house mouse (*Mus* *musculus*) populations after the eradication of rats (*Rattus sp*.) (Harper & Cabrera, 2010; Witmer, Boyd, & Hillis-Starr, 2007). Or when the eradication of browsers has favoured the increase of invasive plants. For example, *Operculina ventracosa*, an invasive vine that was suppressed by goats (*Capra hircus*), spread after the goats' eradication in Sarigan Island (Kessler, 2011).

1.1.2.2 Translocations

Translocations are management tools that involve the human-assisted movement of a living organism from one area with a free release in another. IUCN classify translocations into three types: introductions, when the movement is outside the natural range; re-introduction, when the movement of species is into a native range after extirpation/extinction; and re-stocking when the movement of species is done with the purpose of building up the number of individuals in an area (IUCN, 1987). Translocations are one of the fastest-growing conservation tools for restoring populations of endangered species and improving genetic diversity in small populations (Scott & Carpenter, 1987). They are particularly effective when the movement of species through a founding group takes place with respect to restored areas, typically within the species' historical range (Seddon, Armstrong, & Maloney, 2007; Thévenin, Mouchet, Robert, Kerbiriou, & Sarrazin, 2018). Successful translocations are achieved when a wild source of populations and a high number of animals translocated are released during a long term period (consecutive translocations); and when that release results in low initial mortality and the establishment of a viable and growing population which is able to reproduce and self-sustain (Fischer & Lindenmayer, 2000; Morris, Brook, Moseby, & Johnson, 2021). Since 1990, the numbers of translocations worldwide has increased but these have been focused mainly on vertebrate species (Seddon *et al*., 2007), in particular mammals and birds. Hence, translocations have focused on a small proportion of the world's threatened taxa in comparison with other more abundant animal taxa such as fish and insects (Bajomi, Pullin, Stewart, & Takács-Sánta, 2010; Seddon, Soorae, & Launay, 2005).

Translocations have been a key tool for the population recovery of several endangered species across the globe. One of the more remarkable and noteworthy examples of population recovery associated with translocations has been the case of the black robin (*Petroica traversi*), an endemic passerine to the Chatham Islands. After the whole population was reduced to only five individuals with one breeding pair, three translocations associated with a cross-fostering breeding program managed to increase the population of the robins to a stable level (Butler & Merton, 1992; Kennedy, 2009). More recently, other examples of successful translocations include the reintroduction of North Island robins (*Petroica australis*), saddlebacks (*Philesturnus carunculatus*) (Taylor, Jamieson, & Armstrong, 2005), orange-fronted parakeets (*Cyanoramphus malherbi*) (Ortiz-Catedral, Kearvell, Hauber, & Brunton, 2010), Griffon vulture (*Gyps fulvus fulvus*) (Sarrazin, Bagnolini, Pinna, Danchin, & Clobert, 1994) and Mauritius' kestrel (*Falco punctatus*) (Jones *et al.*, 1995). However, despite the usefulness and increasing rates of translocations around the globe, not all of them are successful. There are some cases where translocations have failed. Causes for failure in translocations are diverse but mainly due to physiological stress (Dickens, Delehanty, & Romero, 2009), management issues (Bubac, Johnson, Fox, & Cullingham, 2019), predation, competition or release in unsuitable areas (Osborne & Seddon, 2012). For example, a translocation of the Australian brown treecreeper (*Climacteris picumnus*), failed due to the long-term effects of translocation related stress (Bennett, Doerr, Doerr, Manning, & Lindenmayer, 2012). Moreover, the Stead's bush wren (*Xenicus longipes)* became extinct because the birds did not survive the translocations to Kaimohu Island after the invasion of ship rats (*Rattus rattus*) on Big South Cape Island, New Zealand (Bell, Bell, & Merton, 2016).

1.1.3 ENDANGERED MIMIDAE ON ISLANDS AS CASE STUDY

The purpose of this section is to identify similarities in the ecology between endangered Mimidae (including my research species) that made them vulnerable to extinction and what have been done to conserve their populations. The family Mimidae is only present in the Americas and includes nine genera comprising over 34 species, 12 of which are restricted to islands (Cody, 2005). Of these, five species are considered threatened, two of which are socially monogamous: the Cozumel thrasher (*Toxostoma guttatum*) and the Socorro mockingbird (*Mimus graysoni);* two species are facultative cooperative breeders: the white-breasted thrasher (*Ramphocinclus brachyurus*) and Hood mockingbird (*Mimus macdonaldi*), and the last species is an obligate cooperative breeder: the Floreana mockingbird (*Mimus trifasciatus*). Below I reviewed the conservation status of the five species of Mimidae categorized as threatened.

1.1.3.1 Cozumel thrasher

The Cozumel thrasher (*Toxostoma guttatum)* is an endemic species of Cozumel Island, Mexico. A 486 Km2 oceanic island located about 17.5 km from the Yucatan Peninsula. The decline of the Cozumel thrasher is not well understood. The two main hypotheses that could explain the population decline of this species are believed to be the impact of successive strong hurricanes and the effect of invasive predators. The first decline in the population was noticed after Hurricane Gilbert in 1988. The species was reported in only four instances in 2001 during extensive monitoring (Macouzet & Escalante-Pliego, 2001). Moreover, the introduction of the exotic boa snake (*Boa constrictor*) in 1971 (Martínez-Morales & Cuaron, 1999) to Cozumel Island where it was not present before, could have accelerated the population decline of this species (Curry, Martínez-Gómez, Hernandez-Molina, & Chacon-Diaz, 2006).

1.1.3.2 Socorro mockingbird

The Socorro mockingbird (*Mimus graysoni)* is an endemic Mimidae from Socorro Island in the Revillagigedos Archipelago, Mexico. The bird faces a decline in the population because a combination of several factors including habitat loss, predation by introduced cats, and competition from other mockingbird species. Habitat loss by intensive sheep grazing has been proposed as the main cause of population decline (Castellanos & Rodriguez-Estrella, 1993). Interspecific competition for resources by a population of the northern mockingbird (*Mimus polyglottos*) does not seem to be one of the reasons due to the segregation of distribution of northern mockingbirds to areas affected by sheep grazing where Socorro mockingbirds are absent (Martínez-Gómez & Curry, 1996). Although the current population is considered viable, its long-term survival is not guaranteed if habitat restoration is not undertaken (Martínez-Gómez, Flores-Palacios, & Curry, 2001). To date, two conservation efforts have been carried out to eradicate two of the main threats for the Socorro mockingbird: an eradication program of feral cats (*Felis catus*) since 2011 (Ortiz-Alcaraz *et al.*, 2017), still ongoing, and the successful eradication of feral sheep (*Ovis aries*) in 2012, showing clear evidence of vegetation recovery on the island after the eradication (Ortíz-Alcaraz *et al.*, 2016).

1.1.3.3 White-breasted thrasher

The white-breasted thrasher (*Ramphocinclus brachyurus*) is a species that has a narrow distribution in the Antilles, with three populations split into two subspecies restricted to the islands of Martinique (*spp. brachyurus*) and Santa Lucia (*spp. sanctaeluciae*). The species is currently listed as endangered by the IUCN, mainly due to the fragmentation and loss of habitat (Mortensen *et al.*, 2017), but the conservation status could be changed to critically endangered and endangered respectively if both subspecies are considered different species as was suggested recently (DaCosta *et al.*, 2019). There is an estimated population of around 1500 individuals across its range (Mortensen *et al.*, 2017). Aside from the loss of habitat, it seems to be that the decline of this species is linked to some aspects of its social system and philopatry. This species is considered a facultative cooperative breeder with an average of 37% of the study population having helpers during a given year (Temple, Hoffman, & Amos, 2009). This implies high philopatry and short/sex-bias dispersal distances reducing the probability of the species to colonize new areas (Temple, Hoffman, & Amos, 2006). In Saint Lucia Island, this species seems to occupy all the suitable habitats and has been positively associated with a native predator distribution (Sass, Mortensen, & Reed, 2017). Meanwhile in Martinique a population viability analysis suggested that the population has enough habitat to ensure population stability if mortality remains low (Mortensen & Reed, 2016). Furthermore, a recent study demonstrated that white-breasted thrashers are likely to respond successfully against brood parasitism of newly arrived species that was believed to threaten their reproductive success (Kramer & Mortensen, 2020).

1.1.3.4 Española mockingbird

The Hood or Española mockingbird (*Mimus macdonaldi*) (Fig. 1.1) is an endemic facultative cooperative breeding bird species of the Galápagos Archipelago (Von Lippke, 2008). In comparison with other Galápagos mockingbirds, Española mockingbirds on Española Island and Gardner-by-Española islet inhabit the coastal areas in larger groups and densities (Curry, 1989). Both populations have a low genetic differentiation due to genetic flow between populations, compared with other Galápagos mockingbirds (Hoeck, Keller, Bollmer, & Parker, 2010). It is considered vulnerable under IUCN criteria because its restricted range and vulnerability to severe stochastic events (Jiménez-Uzcátegui *et al.*, 2019; Wiedenfeld & Jiménez-Uzcátegui, 2008) and the possible introduction of invasive species to the island (Curry, 1986).

Figure 1.1 Hood or Española mockingbird (*Mimus macdonaldi*). Española Island. Photo: Enzo M. R. Reyes.

1.1.3.5 Floreana mockingbird

The Floreana mockingbird (*Mimus trifasciatus*) (Fig. 1.2) is the rarest mockingbird in the Galápagos, with approximately 300 individuals remaining in two islets that represent less than 1% of what was its historical geographic range. The Floreana mockingbird is considered endangered by the IUCN. The species was distributed in the lowlands of Floreana Island but was driven to local extinction in the early 1900s by a combination of factors. The introduction of rodents, specifically Black rats (*Rattus rattus*), to an island that has never hosted a population of native rodents, is considered the main cause of the local extinction of the mockingbird on Floreana Island (Curry, 1986). The species remains in two isolated populations on two different islets off the coast of Floreana. One of the populations is located in the 10 ha islet of Champion, supporting a population that ranges between 20 to 30 individuals with a low genetic diversity expected for a small island (Hoeck, Keller, Beaumont, *et al.*, 2010; Hoeck, Keller, Bollmer, *et al.*, 2010). The other population is located on Gardner-by-Floreana a 76.5 ha islet holding a population of around 250 individuals. Until recently, the Floreana mockingbird had been one of the least studied species in the Galápagos due to the inaccessibility of the islets where they remain. Recent research on the Floreana mockingbird has investigated: the genetic management of the species (Hoeck, Keller, Beaumont, *et al.*, 2010), population dynamics (Grant, Curry, & Grant, 2000; Jiménez-Uzcátegui, Llerena, Milstead, Lomas, & Wiedenfeld, 2011), modelling methods to reintroduce the species considering it as a socially monogamous (Bozzuto, Hoeck, Bagheri, & Keller, 2017), health status through blood measurements (Deem, Parker, Merkel, Cruz, & Hoeck, 2011), and some breeding diet notes that were recorded in a short observation period (Ortiz-Catedral, 2014). Currently, the species will be reintroduced to Floreana Island (Ortiz-Catedral, 2018), if the eradication of invasive mammals and ecological restoration of the island is successful (Island Conservation, 2013). Despite all the studies on the Floreana mockingbird, there are still many aspects of its biology that remain unknown in particular, accurate demographic estimation, and studies of its social structure, dispersal, and optimal habitat use. There is urgency for better knowledge of these topics for Floreana mockingbirds to support the success of reintroduction and ensure the establishment and successful reproduction of the future reintroduced population.

Figure 1.2 Adult Floreana mockingbird (*Mimus trifasciatus*), Champion Islet. Photo: Enzo M. R. Reyes.

1.1.4 THE GALÁPAGOS ISLANDS

The Galápagos Islands is an archipelago 1000 km off the west coast of Ecuador, globally renowned as one of the most well preserved tropical archipelagos in the world (Dvorak, Vargas, Fessl, & Tebbich, 2004; Jimenez-Uzcategui *et al.*, 2007). Conservation management in the Galápagos Islands faces a multitude of challenges due to the vast number of introduced species. It has been reported that 18 invasive vertebrates are established on one or more of the islands. Of these, rats (*Rattus rattus* and *R. novergicus*), mice (*Mus musculus*), and cats (*Felis catus*) are suggested as main drivers for local vertebrate extinctions and extirpations on the islands (Fundacion Charles Darwin & WWF Ecuador, 2018). A total of 29 populations and species of native terrestrial vertebrates have disappeared in the Galápagos during the Holocene (Steadman, Stafford, Donahue, & Jull, 1991). Recently, Carmi *et al.* (2016) reported what could be the first modern extinction in the archipelago, having divided the Galápagos vermillion flycatcher into two cryptic species, one of which was endemic to San Cristobal Island (*Pyrocephalus dubius*) and is possibly extinct because of introduced mammals and parasites.

From all the inhabited islands in the archipelago, Floreana Island (17300 ha) has been the most impacted by introduced species causing a loss of several species and subspecies (Dvorak *et al.*, 2017; Jiménez-Uzcátegui & Ortiz-Catedral, 2020). Floreana Island is home to at least 18 endemic species including a lizard and several land snails (Island Conservation, 2013). Regarding birds, from the 22 terrestrial species that were originally present on Floreana, 10 have been extirpated or will soon become locally extinct (Dvorak *et al.*, 2017). The Floreana mockingbird was extirpated from Floreana just 50 years after the visit of Charles Darwin to the Galápagos (Curry, 1986). To date, Floreana has been identified as one of the highest-ranked islands in the world (in position number six) where eradication of invasive mammals could feasibly commence by 2020 (Holmes *et al.*, 2019).

1.1.4.1 Bird translocations in the Galápagos Islands

Overall, five translocations attempts of different species have been carried out on the Galápagos. Two species of reptiles (*Conolophus sp. and Chelonoidis sp.)* have been successfully translocated between islands. Meanwhile, for the birds, the translocation success is controversial for the two species translocated: Galápagos hawk (*Buteo galapagoensis*) and the Mangrove finch (*Camarhynchus heliobates*).

The Galápagos hawk reintroduction was part of the restoration project of Pinzon Island carried out by the Galápagos National Park. The principal objective was the eradication of the Black rat (*Rattus rattus*) using the rodenticide brodifacoum TM. Pinzon island is 1800 ha and has three species of endemic reptiles and six species of endemic land snails. The restoration project on this island was designed to allow the successful breeding and recruitment of the endemic Pinzon Island tortoise (*Chelonoides ephippium*) that was affected due to predation by rats (Rueda *et al*., 2019) as well as assisting in the recovering of the endemic Pinzon racer (*Pseudalsophis slevini*) and an endemic undescribed gecko (Ortiz-Catedral pers. communication). To avoid the possibility of the Galápagos hawks' extirpation on Pinzon Island because of poison by-catch (consuming poisoned rats), 60 hawks were taken to Santa Cruz Island and held in captivity. A short period after the successful eradication, the individuals were released back to the original island some of them with radio transmitters. Between 12 and 170 days after the birds' release, mortality was observed in 22 of 32 tracked Galápagos hawks due to toxicosis (Rueda, Campbell, Fisher, Cunninghame, & Ponder, 2016). The remaining live individuals (10) were recaptured, received veterinary care and held in captivity until the residual poison on the island dissipated (Rueda *et al*., 2019).

In the case of the Mangrove finch, a translocation of nine individuals (mostly juveniles) from Playa Tortuga Negra on the west coast of Isabela Island to Bahia Urbina was carried out by the. End of May, 2010. The team monitored the birds using a radio-telemetry system and by repeated sightings of individuals identified by particular colour combination bands. Of the birds moved, one died, four returned to the original population source and the status of the four others was unknown (Cunninghame, Young, & Fessl, 2011). Currently, translocations were abandoned in favour of the head-starting technique where 39 hand-reared individuals have been released into the wild with a high percentage of survival and recruitment (Bulgarella, Quiroga, & Heimpel, 2019).

1.2 JUSTIFICATION OF THE PROJECT

Globally, there appears to be a high rate of failed reintroductions especially for locally endangered species (Bubac *et al.*, 2019; Griffith, Scott, Carpenter, & Reed, 1989). The rate of failure seems to be associated with the prevalence of invasive species, mainly in the Oceania region despite the success of translocations to predator-free areas in New Zealand (Morris *et al.*, 2021). To date, the proportion of failed translocation is difficult to determine because most of the failures are poorly documented or not published in peer-reviewed articles (Malone *et al.*, 2018). Further, there is a lack of consensus about what defines a "successful reintroduction" (Fischer & Lindenmayer, 2000; Morandini & Ferrer, 2017; Sutherland *et al.*, 2010). A review of different conservation translocations shows that 20.9% of reintroductions are categorised as failed, 54% as successful and 25.1% as an unknown outcome (Bubac *et al.*, 2019). Regarding specific taxa, it is reported that one-third of reintroductions (published) failed in freshwater macroinvertebrates (Jourdan *et al.*, 2019), 42% in freshwater fish (Cochran-Biederman, Wyman, French, & Loppnow, 2015), 59% for amphibians and reptiles (Germano & Bishop, 2009), 48% for plants (Godefroid *et al.*, 2011), 60% and 85% of translocations have failed for both mammals and birds respectively (Bubac *et al.*, 2019). However, the data might not reflect the real percentages because of the geographic bias of the translocations attempts (Seddon, Griffiths, Soorae, & Armstrong, 2014).

In a series of 291 reintroduction cases of different taxa assessed by IUCN (Soorae, 2008, 2010, 2011, 2016, 2018), 41% of the reintroductions fall into the categories of partially successful or failed. Most reintroductions failed due to multiple factors that included poor scientific understanding about the ecology of target species, poor quality of the habitat designed for the reintroduction, lack of effective predator control or failure to eliminate the original cause of threat before the reintroduction and because of unstructured planning and lack of subsequent monitoring (Bubac *et al.*, 2019; Griffith *et al.*, 1989; Sheean, Manning, & Lindenmayer, 2012; Veitch, 1995).

For birds, most reintroductions have been done on monogamous species with uniparental or biparental care with some few exceptions of cooperative breeders (Table 1.1). Cooperative breeders represent a challenge for these kinds of conservation methods as one of the main aspects to be considered before a reintroduction is the composition of the founder group through familiarity and relatedness of the individuals (Armstrong & Craig, 1995). Cooperative breeding birds are defined as birds that live in social units composed of one or more breeding birds plus one or more non-breeding helpers (Brown, 1987). There are many hypotheses explaining this reproductive adaptation, however, the most accepted are the “habitat saturation” hypothesis in which helpers remain in a state of reproductive suppression due to the shortage of breeding opportunities (Brown, 1974, 1987; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992) and the “life history” hypothesis where species with non-migrant behaviours, favourable environmental conditions, decreasing mortality and fecundity are more likely to display cooperative breeding behaviours (Arnold & Owens, 1998; Rowley & Russell, 1990; Russell, 1989).

Although cooperative breeding birds are not over-represented among the most endangered birds on the planet (Walters, Cooper, Daniels, Pasinelli, & Schiegg, 2004), there have been few cases of translocations with varying degrees of success. (Table 1.1). One of the principal outcomes of these translocations has been the disruption of the social system. The translocated birds become social pair breeders without helpers in the first stages of the translocation (Armstrong, Lovegrove, Allen, & Craig, 1994; Carrie, Conner, Rudolph, & Carrie, 1999; Komdeur *et al*., 1995; Mumme & Below, 1999). Only two cases of all the translocations summarized in Table 1.1 didn’t change their social systems. This was because of the birds being relocated as entire family groups or due to some aspect of the breeding biology of the species (Bennett *et al*., 2012; R. H. Clarke, Boulton, & Clarke, 2002)

Table 1.1 Cases of reintroductions in cooperative breeding birds

Species	Country	Number of translocations	Source
Black-eared miner (*Monarina melanotis*)	Australia	1	Clarke *et al*., (2002).
Brown treecreeper (*Climacteris picumnus)*	Australia	2	Bennett *et al*., (2012); Cooper & Walters (2002).
Florida scrub-jay (*Aphelocoma coerulesces*)	USA	1	Mumme & Below (1999).
Noisy miner *(Manorina melanocephala*)	Australia	1	Clarke and Schedvin (1997).
Red-cockaded woodpecker (*Picoides borealios*)	USA	6	Carrie *et al*., (1999); Cox & McCormick (2016); Franzreb (1999); Herbez, Chamberlain, & Wood (2011); Rudolph, Conner, Carrie, & Schaefer (1992); Wallace & Buchholz (2001).

Seychelles warbler (*Acrocephalus sechellensis*)	Seychelles	3	Komdeur *et al*., (1995); Wright, Shah, & Richardson (2014).
Whitehead (*Mohoua albicilla*)	New Zealand	4	Armstrong *et al*. (1994), Igic *et al*. (2010), Parker (2013).

The future translocation of the Floreana mockingbird (Fig. 1.3) represents an ideal management system for further investigation. The species has a complex social system and habitat requirements, inhabits an environment of differing quality, under often extreme and very variable climate conditions, and lives in social groups as cooperative breeders in closed populations. The species is also long-lived, which make possible the collection of temporal observations of the same individual in different ecological times. Furthermore, Floreana mockingbirds are naïve to humans (curious with no fear towards humans), and endangered birds under the criteria B1ac(iv)+2ac(iv) of IUCN that gives this species considerable conservation value and justification for the reintroduction to Floreana Island.

Figure 1.3 Social group of Floreana mockingbird on Champion Islet. Photo: Enzo M. R. Reyes

1.2.1 THESIS OUTLINE

In this thesis, I explore questions related to the population dynamics, behaviour and ecology with the overarching aim of facilitating their reintroduction to the island of Floreana. My thesis is divided into five chapters, two descriptive chapters (introduction and conclusion) and four research chapters. Each research chapter is presented in a publication format (intended journal mentioned in parenthesis below) with their respective sections. Despite the study area being detailed in the methods section of each chapter, I am attaching a description and real photographs of the study area in appendix 1.

In chapter 2 (*Ornitologia Neotropical*), I developed a species-specific tool for easy sexing of the Floreana mockingbird on the field, using a statistical method and morphology. In chapter 3 (*Conservation Biology*), I addressed the gap in knowledge related to the demography of the Floreana mockingbird in both populations since the categorisation of the Floreana mockingbird as an endangered species. I conducted a detailed analysis of the population dynamic of the species using capture-mark-recapture models (CMR) in program Mark (White & Burnham, 1999) to answer the following questions:

What is the apparent survival probability for each year?

What is the recruitment rate in each of the two populations studied?

How large is the population on each of the two islands studied?

Is the population on each of the two islands stable or decreasing?

In chapter 4 (*Plos One*), I examined the cultural divergence of the species between the two extant populations. I conducted recordings of the different vocalizations of the species and analysed them using KOE (Fukuzawa *et al*., 2020) with the aim of responding to the following questions:

Is there a song divergence between the two extant populations?

What are the factors that explain the song divergence between the populations?

In chapter 5 (*Behavioural Ecology*), I investigated the hierarchy, structure and disruption of the dominant social network of the Floreana mockingbird. I used the transitive triangle method to classify hierarchy structure and exponential random graph models (ERGM) among family groups to investigate the structure of a dominant social network. Finally, I simulated different scenarios of harvesting for reintroduction with the aim of identifying the likelihood of social collapse by removal of important individuals in the network. This chapter address the following questions:

Do Floreana mockingbirds have a linear hierarchy?

Are patterns of dominance influenced by individual attributes or sexual difference?

Will the removal of key individuals influence the social collapse of the social network?

The thesis outlined here contributes to novel understanding and fills significant research gaps in the biology of Floreana mockingbirds in both populations on Champion and Gardner-by-Floreana. In addition, the findings of this thesis will provide information and protocols to the Galápagos National Park with regards to the adequate management and planning for the future reintroduction of this bird, considering all the variables related to the bird ecology, to ensure successful reintroduction of the species.

1.3 COVID 19 STATEMENT

The following thesis was planned to include three years of field research as part of a four-year doctorate programme. However, due to conditions and travel restrictions imposed because of the COVID 19 global pandemic, data collection was undertaken only in 2019. Field trips planned for 2020 and 2021 (two field trips each year) were cancelled. I was directly affected by the cancellation of the field trips to the study area (detailed below) and the withdrawal of funding by an NGO that had previously granted me funding, which was impacted by the financial crisis brought about by COVID 19. Data collected for some of the research chapters was not sufficient to conduct a robust analysis, particularly for the social network research chapter. To reach strong conclusions regarding the sociality and social cohesion of the family groups of the Floreana mockingbirds, at least one year of behavioural observation in the two seasons of the Galápagos islands would have been necessary. Ideally, two years of behavioural observation (cyclic observations) would have been conducted. For the same reason, one of the originally proposed research chapters (habitat requirements) was removed from the thesis outline presented in my confirmation report in 2019. The chapter was removed as the data collection was to have taken place in March 2020 at the beginning of the pandemic. Fortunately, demographic and vocalization data were enough to conduct robust statistical analysis. Notwithstanding the hardship of COVID 19 and the emotional consequences of the lockdown, I also faced the uncertainty of the College of Sciences financial situation that ended with the permanent separation of my main supervisor from Massey University and forced me to finish before the due date of my doctorate program to avoid any future adversity.

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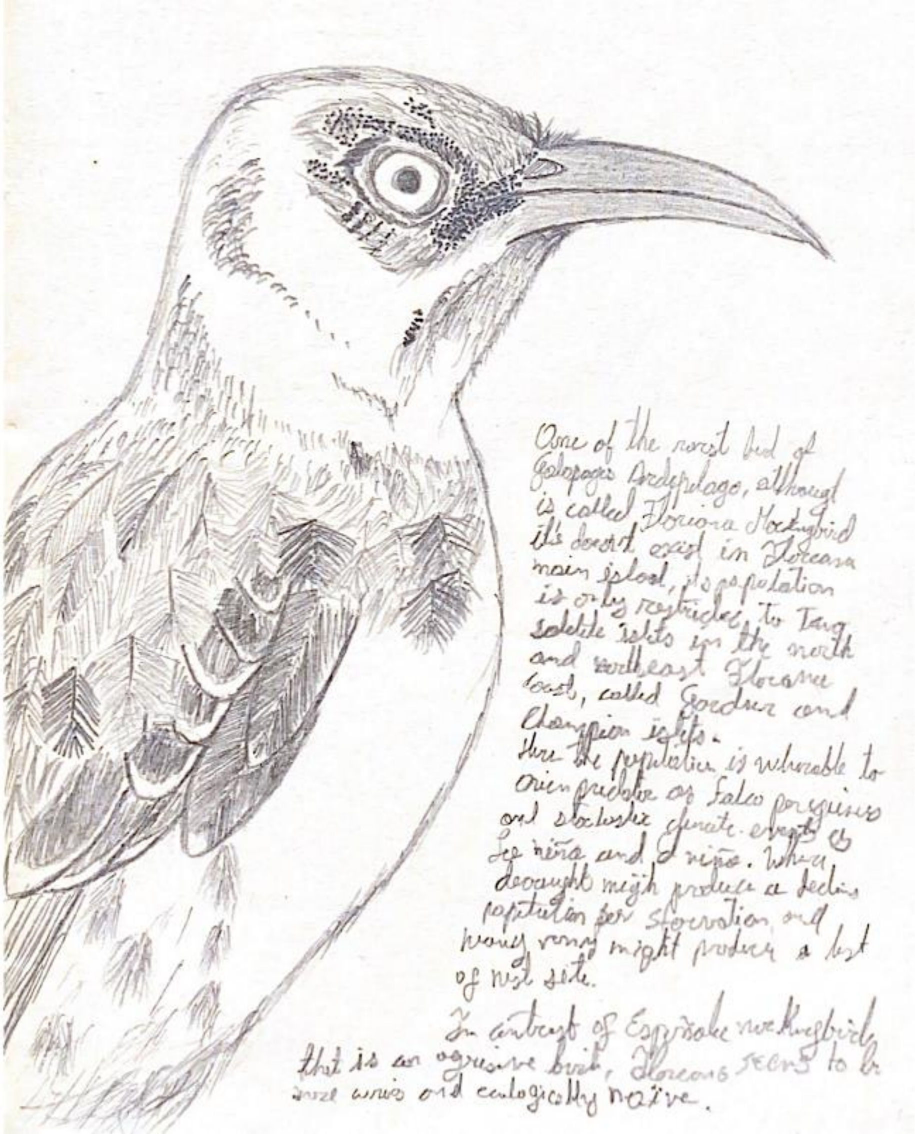
Chapter 2

Sexing of the endangered Floreana mockingbird (*Mimus trifasciatus*) using morphometric measurements



One of the rarest bird of
Galapagos Archipelago, although
is called Floreana Mockingbird
it's doesn't exist in Floreana
main island, its population
is only restricted, to Tiny
satellite islets in the north
and northeast Floreana
coast, called Gardner and
Champion islets.
Here the population is vulnerable to
alien predator as Falco peregrinus
and stochastic climate events as
La niña and El niño. When
drought might produce a declin
population per starvation and
heavy rainy might produce a lost
of nest site.
In contrast of Española mockingbird
that is an agressive bird, Floreana seems to be
more wary and ecologically naive.

Meeting the Floreana mockingbird for first time

Champion Islet, December 2016

Enzo M. R. Reyes

2.1 SEXING OF THE ENDANGERED FLOREANA MOCKINGBIRD (*MIMUS TRIFASCIATUS)* USING MORPHOMETRIC MEASUREMENTS

Enzo M. R. Reyes[1,4,*], Smith, A.N.H.[1], Rueda, D.[2], Sevilla, C.[2], Brunton, D. H.[1] & Ortiz-Catedral, L.[1,3]

[1] Ecology and Conservation Lab, School of Natural Sciences, Massey University, Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand.

[2] Galápagos National Park, Puerto Ayora, Galápagos, Ecuador.

[3] World Parrot Trust, Glanmor House, Hayle Cornwall TR27 4HB, United Kingdom.

*Corresponding author: enzorreyesb@gmail.com

SEXING OF THE FLOREANA MOCKINGBIRD

2.1.1 ABSTRACT

Male and female adult Floreana mockingbird (*Mimus trifasciatus*) have monomorphic plumage features that make them impossible to assign to a sex category in the field. In this study, we use discriminant function analysis (DFA), a widely used technique, to assess the best measures to use to determine sex. We measured six morphological characteristics (weight, bill depth, bill width, tarsus, wing chord, and head-bill) for birds of known sex (determined by molecular techniques) from the two extant populations of Floreana mockingbird on Champion and Gardner islets, within the Galápagos archipelago. Using a coefficient of sexual dimorphism, we found that males are significantly larger than females in five of the variables. Discriminant functions using wing and a combination of wing-weight and wing-tarsus could classify birds with a 98% level of accuracy. Furthermore, we were able to estimate a robust cut-off point to determine the sex of individuals on the field through a decision tree, using only wing chord as morphological variable. Fast and accurate sexing of the bird based in one variable will reduce handling times and minimise stress for captured birds. A robust sexing technique will also provide conservation practitioners with a management tool when assessing population viability of this endangered cooperative breeding bird and implementing it in the reintroduction plan.

Sexado de una especie en peligro de extinción: el Cucuve de Floreana (*Mimus trifasciatus*), usando medidas morfométricas.

2.1.2 RESUMEN

Machos y hembras adultos del Cucuve de Floreana (*Mimus trifasciatus*) poseen características monomórficas con respecto al plumaje, haciendo imposible sexarlos en el campo. En este estudio nosotros usamos un análisis de función discriminatoria (DFA en inglés) una técnica ampliamente usada para determinar el sexo. Basándonos en la morfometría de seis medidas externas de adultos (peso, profundidad del pico, ancho del pico, tarso, cuerda alar, and cabeza incluido pico) de sexo conocido de las dos únicas poblaciones de la especie Champion y Gardner en las islas Galápagos. Usando un coeficiente de dimorfismo sexual, encontramos que los machos son significativamente más grandes que las hembras en cinco de los rasgos morfológicos. Funciones discriminatorias usando las medidas del ala y una combinación de ala-peso y ala-tarso pudieron clasificar las aves con un 98% de precisión. Además, fuimos capaces de estimar los puntos de corte para determinar el sexo de individuos en el campo a través de un análisis de decisiones de árbol usando cuerda alar como una sola variable morfológica. El Sexado rápido y correcto basado en una sola variable prevendrá el estrés innecesario causado por la manipulación de la especie. Una técnica robusta de sexado preverá a los conservacionistas con una herramienta de manejo para la evaluación de la viabilidad poblacional de esta especie en peligro de cría cooperativa e implementación en el plan de reintroducción de la especie.

Key words: Sexing, Discriminant Function Analysis, Floreana mockingbird, Morphometry, Conservation, Galápagos Islands.

2.2 INTRODUCTION

Identifying the sex of individuals is important in ecology research and conservation biology because knowing the sex of birds can tell us about possible biases in the population sex ratios and improve our knowledge of the population dynamics of endangered species. For example, in many populations, one sex may have higher mortality rates than the other causing a bias in the operational sex ratio of a population and potentially lowering population growth rates (Brekke, Bennett, Wang, Pettorelli, & Ewen, 2010). An efficient method for sexing monomorphic species can also improve protocols and methodologies for translocations and captive breeding programs. In addition, the correct interpretation of behavioural and ecological data often relies on knowing the sex of the study individuals. Many avian species can be sexed using obvious external phenotypical factors such as size and colour dimorphism; features usually correlated with social mating systems (Dunn, Whittingham, & Pitcher, 2001; Owens & Hartley, 1998) or by observing sex-specific behaviours (Joo, Ha, Jeong, & Yoon, 2018; Lewis *et al.*, 2002). However, for monomorphic species or juvenile birds, differences are less obvious and considerable overlap in male and female characteristics can cause uncertainty. When sex-specific behaviours are used foe assigning sex, observers may need long periods of observations that are time-consuming and logistically expensive, especially in areas of difficult access.

For sexing monomorphic species, with an absence of sexually dimorphic external factors, a variety of techniques have been proposed. These techniques include both invasive and non-invasive methods as cloacal inspection, molecular analysis, vocalizations and statistical methods based on morphometrical measurements, and combinations of all of these (Bazzano, Leche, Martella, & Navarro, 2012; Bourgeois *et al.*, 2007; Ellrich, Salewski, & Fiedler, 2010; Lessells & Mateman, 1998; Morinha, Cabral, & Bastos, 2012; Volodin *et al.*, 2009). Of these methods, one of the most reliable in sexing birds has been the use of discriminant function analysis (DFA) morphometric measurements. This technique has been used widely in different birds taxa from Procellariforms (Mischler, Bell, Landers, & Dennis, 2015) to passerines including species of Mimids (Fuchs & Montalti, 2016; Martínez-Gómez & Curry, 1998), even in juvenile birds (Martín, Alonso, Alonso, Morales, & Pitra, 2000; Thorogood, Brunton, & Castro, 2009). This method identifies individuals of known sex by creating a linear function of measurements that best discriminates between males and females (Phillips & Furness, 1997) and the coefficient outputs can be used to generate an equation to classify the sex of further sampled individuals (Queen, Quinn, & Keough, 2002). Nevertheless, despite the wide use of the method, there are some caveats in the robustness of discriminant equations when using small sample sizes (Dechaume-Moncharmont, Monceau, & Cezilly, 2011). Moreover, although easy to understand by experts, the equations may be problematic for use by those without an academic background involved in citizen science or community conservation.

The Floreana mockingbird (*Mimus trifasciatus*) is the rarest and most range-restricted mockingbird species in the Galápagos archipelago and is classified as “endangered” by the UICN. Historically, Floreana mockingbirds occurred in the lowlands of Floreana Island and its surrounding islets. Floreana mockingbirds disappeared in the early 1900s, due to a combination of factors, in particular, the effects of introduced species (Curry, 1986; Hoeck *et al.*, 2010). Currently, the Floreana mockingbird is restricted to two islets representing less of 1% of its former range. Because of its rarity (less than 350 individuals) and the inaccessibility to these islets, the ecology of the Floreana mockingbird is little known, which has prevented the development of management plans directed towards increasing the number of individuals and populations, in particular via reintroduction of birds to the lowlands of Floreana Island. Despite its relevant role in the history of biology (Hoeck *et al*., 2010) and its conservation importance (Ortiz-Catedral, 2018), basic aspects of the natural history of this species are still missing. Although there are existing criteria using the wing chord for sexing Mimids in the Galápagos, most of these criteria have been developed based in the morphometric characters of a different species, the Galápagos mockingbird (*Mimus parvulus*) (Curry, 1988, 1989; Curry & Grant, 1989; Kinnaird & Grant, 1982). To date for the Floreana mockingbird, sex determination has been mentioned in Grant, Curry & Grant (2000) and in Deem *et al* (2011) but neither of these publications report specific criteria to determine the sex of this species using morphometric measurements. Our goal was to determine whether morphological differences could be used to distinguish between the sexes of Floreana mockingbirds in discriminant function analysis to correctly determine sex. We then used a decision tree analysis to identify the trait(s) that provided the most discriminatory power and estimated cut-off points of morphological measurements that could be easily interpreted in the field.

2.3 METHODS

2.3.1 Study site

This study was conducted on Champion (90° 23’100’’W 01° 14’240’’S) and Gardner-by-Floreana (90°17’700’’W 01°19’969’’S) islets in the northern part of Floreana Island (Fig. 2.1). Champion is a 9.4 ha circular islet (~ 400 m diameter). It is a crater emerged from the seafloor whose maximum elevation is 46 meters above the sea and is located less than one kilometre away from the coastline of Floreana Island (Grant *et al*., 2000).

The Gardner-by-Floreana islet (76.5 ha) is located eight Km away from the coast of Floreana. It is a big volcanic cone that has partially sunk, creating an islet covered by cliffs of 50 to 100 m high and reaching an elevation of 210 meters above sea level. The islet has a 100 m high plateau of approximately 12 ha located in the eastern part of the islet (Jiménez-Uzcátegui, Llerena, Milstead, Lomas, & Wiedenfeld, 2011) that is the only place accessible and safe for humans.

2.3.2 Morphometry and molecular sexing

Birds were captured as part of an annual long-term monitoring study carried out since 2006. During November 2015, a total of 41 birds (24 males and 17 females) were caught using a wire cage trap with a lure; these birds were then banded (permit 025-MAE-DPNG-IA), measured and released. The following morphological body measurements (Fig. 2.2) were taken: (1) mass; (2) bill depth, in vertical plane in the middle of the nares; (3) bill width, in the upper mandible in a horizontal plane in the anterior edge of the nares; (4) tarsus, from the intertarsal joint to the foot joint; (5) wing chord, with the wing in a natural arc and at 90° angle with the radius/ulna; (6) head-bill, from the upper bill tip to the nape. All measurements were taken to the nearest 0.1 mm using a stopped wing ruler and Vernier callipers, the mass was taken to the nearest 0.5g using a 50g or 100g Pesola spring balance. All measurements were taken twice and averaged prior to knowing the sex of each bird, which was later confirmed by molecular analysis of DNA for each bird. For DNA samples, we used a needle to prick blood from the brachial vein of each adult mockingbird shortly after the capture. Approximately 5 μL of blood was collected from each individual using a capillary tube and the blood was stored in a *CryoTube*^{TM} vial with 1.0 ml of Queen’s Lysis buffer. Vials were labelled with their respective metal band identity of each sampled bird. Blood samples were sent to the Equine Parentage and

Animal Genetic Services Centre, Massey University, New Zealand for molecular analysis of the CHD gene of the avian sex chromosomes using a similar technique described in Norris-Caneda & Elliott (1998). Blood samples were taken under permit number 025-MAE-DPNG-IA from the Galápagos National Park and Ecuadorian Ministry of Environment. Import permits to New Zealand were granted by the Ministry of Primary Industries under permit number CL8861 from MPI CUSMOD Release AF100101064522.

2.3.3 Analysis

Assumptions of normality were tested using a Shapiro-Wilk Test in R (R Core Team, 2013). All variables met the condition of normality so no transformation was carried out. We did not remove outliers from the data set because of the small sample size, especially for females. To test for inter-sexual differences among the molecular sexed birds, we used an unpaired t-test for each pair of measurements. Moreover, for each measurement, we calculated the percentage of sexual dimorphism using the formula described in Holmes & Pitelka (1968): 100x(m-f)/m, where m and f are the mean values of the male and female respectively. Discriminant function analysis (DFA) of the measurements of the known sex birds were then conducted to determine which measurements were most reliable for classifying individuals either as male or female. Wilks' lambda (λ) statistics was used as a variable selection criterion. The accuracy of our discriminant functions were determined by the percentage of known sex individuals correctly classified using all the individuals. In addition, we applied a jack-knifing prediction procedure in which each case was reclassified by repeatedly removing a single individual and then classifying this individual based on the discriminant function generated by the remaining birds. When we obtained the best discriminant functions we then calculated the cut-off points of probabilities of being a male or female through a decision tree analysis in R (R Core Team, 2013). The analyses were run on R using the packages *MASS*, for the LDA calculations, *rrcov* for the multivariate lambda values and packages *rpart, GGally* and *tidyverse* for the decision tree analysis. Univariates lambda values were extracted from *SPSS* software (IBM, 2020).

2.4 RESULTS

We sampled 14 birds from Champion (nine males and five females) and 27 birds from Gardner (15 males and 12 females). Morphological measurements from the 41 birds that were molecularly sexed showed that males and females overlapped but, generally males were larger than females, revealing sexual dimorphism by size (Table 2.1; Fig. 2.3). The mean values for four traits - weight, bill depth, tarsus and wing, were significantly larger in males than in females. The DFA shows that the wing trait performs the best as a single variable classifying birds correctly 98% of the time (Table 2.2). We created four discriminant functions using a combination of the variables wing + weight, wing + tarsus, wing + all beak and all measurements combined. From which wing + weight and wing + tarsus classified birds correctly 98% of the time in both cases and had a greater discriminatory power based on the Wilks' Lambda values (Table 2.2). As wing performed the best as a univariate, the calculated cut-off point by a decision tree analysis was 119.5. The probability of correctly classifying as a female was 94% under the threshold of 119.5 cm, and 100% probability of correctly classifying as a male when the wing is equal or major than 119.5 cm. The cut-off point for tarsus was 39.85. The probability of correctly classifying as a female was 85% under the threshold of 39.85 cm, and 79% probability of correctly classifying as a male when the tarsus is equal or major than 119.5 cm. Furthermore, for weight, we obtained two cut-off points: 61.6 and 56.65. Birds under 61.6

and 56.65 g could be classified as females with 59% and 77% probability, respectively. Meanwhile, birds equal or major than 56.65 and 61.6 g could be classified as males with 56% and 100% probability, respectively.

2.5 DISCUSSION

In this study, we investigated whether Floreana mockingbirds can be correctly classified as a male or female by morphological measurements and, if so, which morphological traits are the best to assign a correct classification. We concluded that male and female Floreana mockingbirds can be easily identified using simple morphological measurements. Our results confirm the assumption of Deem *et al.* (2011) that these monochromatic species present sexual dimorphism based on the size of morphological traits. Males were significantly larger than females in five of six morphological traits except beak width; similar features have been present in other two mockingbirds species: *M. saturninus* and *M. triaturus* (Fuchs & Montalti, 2016). Although, when using the coefficient of sexual dimorphism, the weight seems to be the more dimorphic trait, weight differences were not enough to correctly assign sex using the DFA. Male and female Floreana mockingbirds can be distinguished with 98% accuracy using only wing or a combination of wing, weight and tarsus.

Despite the widespread use of DFA, some factors can affect its performance. One of them is the consistency of the observer when taking the morphometric measurements. Some studies of sexing by morphological traits have found that this parameter can create bias in the results (Henry, Biquand, Craig, & Hausberger, 2015). Here, our morphological measurements were taken by a single observer at both sites during the same period of time, thus reducing the likelihood of introducing bias to our analysis. Other disadvantages are that DFA can only be applied in populations with a small degree of geographic variation and only over a certain time frame due to the potential for temporal instability (Ruiz, González-Solís, Oro, & Jover, 1998; Shealer & Cleary, 2007). In the case of the Floreana mockingbird, although there was a difference in morphology between populations (Chapter 4) most of the significant differences were related to the beak measurements, hence the usefulness of using wing chord as a sexing method for both populations. However, our results may lose efficacy in the future if temporal variation in morphometric traits occurs, a factor that has been shown in other Galápagos passerines (Gibbs & Grant, 1987).

We recommend the use of wing chord as a simple trait because the accuracy of classification was over 90% and because this measurement has been widely used in other mockingbird species (Curry, 1988, 1989; Curry & Grant, 1989; Fuchs & Montalti, 2016; Kinnaird & Grant, 1982; Martínez-Gómez & Curry, 1996, 1998). We note that tarsus has been used in other birds to classify sex but it was not as effective as in our results (Montalti, Graña-Grilli, Maragliano, & Cassini, 2012; Taylor & Jamieson, 2007). Additionally, we do not recommend the use of weight alone as a discriminant for sex because weight varies seasonally and is also dependent on the time of day of the measurement (Lehikoinen, 1987). Nevertheless, the use of a single measurement has the added benefit of minimize handling time reducing stress. An important factor that needs to be considered when handling endangered species (Currylow, Louis, & Crocker, 2017; Dechaume-Moncharmont *et al.*, 2011). Moreover, the wing is an easy trait to measure because the landmarks are well-defined and because of its size in comparison with other morphological traits in passerine birds. Bigger traits are easy to measure regardless of the observer's experience reducing measurements errors (Yezerinac, Lougheed, & Handford, 1992). One caveat is that our results can only be applied in non-moulting adults when using the wing only. Although not reported for the Floreana mockingbird yet, some passerines species show differentiation between the wing size of juvenile individuals, which have shorter and rounded wings when compared to adults (Green, Whitehorne, Taylor, & Drake, 2009; Norman, 1997).

The main goal of this study was to develop a tool that could be easily interpreted and applied by the personnel of the Galápagos National Park. This tool does not rely on equations of the discriminant functions but instead, we present thresholds on key measurements, easy to understand and quick to apply. Monitoring of the Floreana mockingbird and access to the study sites are restricted due to the conservation status of this species. Access to scientists only occurs for a limited number of days and a limited number of people. Meanwhile, park-rangers of the Galápagos National Park have free access to monitoring the study sites and hence the need for an easy and quick tool for the monitoring of this endangered species.

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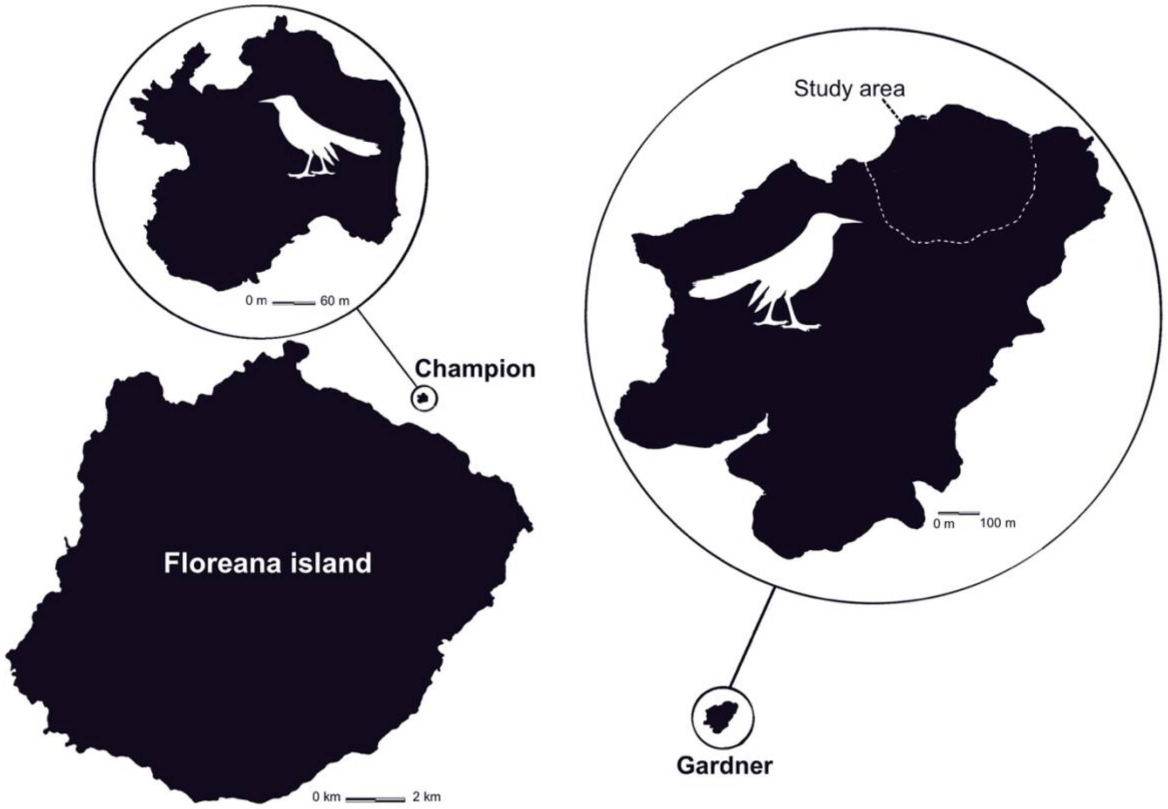

Figure 2.1 Location of the Floreana mockingbird populations. For the Champion population, the study area corresponds to the whole islet. For the Gardner population the dotted area indicates the 12 ha study which is the only area accessible on the island.

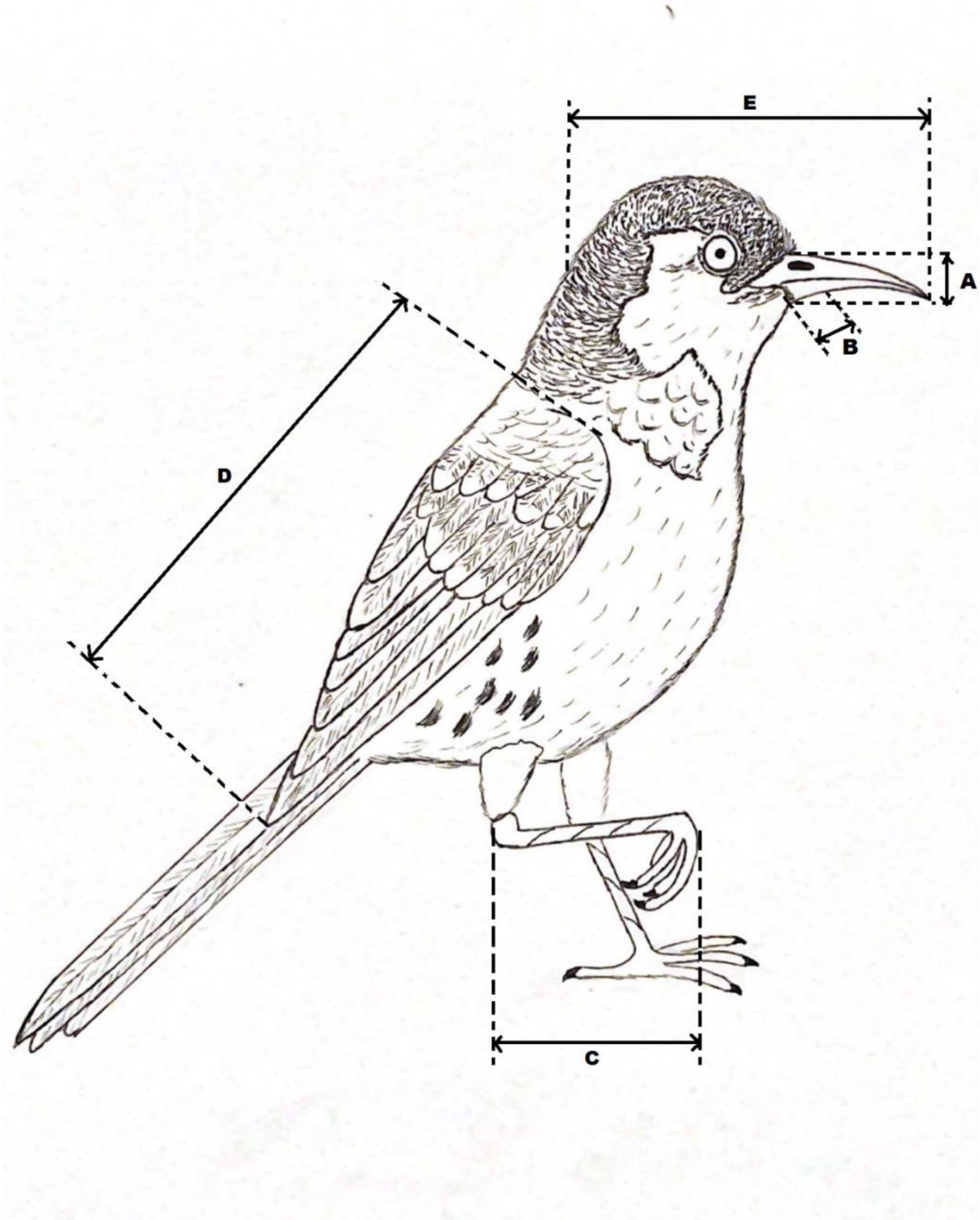

Figure 2.2 Summary of morphological measurements used for the sexing of the Floreana mockingbird. a) bill depth, b) bill width, c) tarsus, d) wing chord, and e) head-bill. Drawing by: Enzo M. R. Reyes.

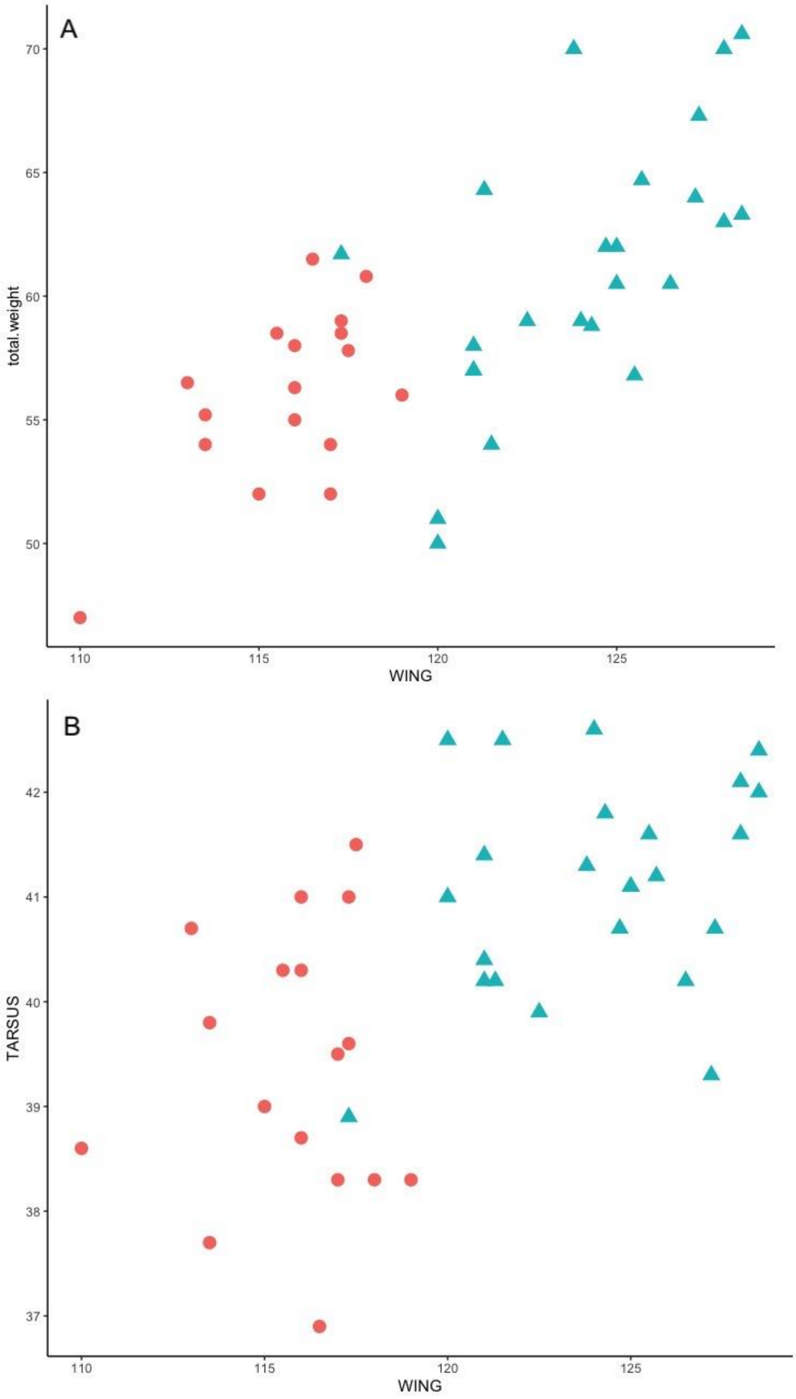

Figure 2.3 Plot of the measurements used as discriminant functions that best predict the sex of the Floreana mockingbird. A) Wing and weight and B) wing and tarsus measurements for male (triangles) and females (circles) Floreana mockingbird. Wing and tarsus measures are given in mm, while weight is given in g.

Table 2.1 Morphological measurements of 41 Floreana mockingbirds sexed using molecular methods and percentage of dimorphism for each morphological trait. Unpaired t-test values, df and significant values are given for comparison of variables between sexes. NS = not significant; *** significant at <0.001. Length measurements are given in mm, while weight is given in g.

	Males			Females			Males vs Females		
	Mean ± SD	Range	N	Mean ± SD	Range	N	t	df	% Dimorphism
Weight	61.02 ± 5.45	50-70.6	24	56 ± 3.57	47-61.5	17	3.56***	38.85	8.23
Head-beak	59.25 ± 1.22	56.2-61	24	57.96 ± 0.67	57-59.1	17	4.29***	37.01	2.18
Width	7.14 ± 0.46	6.4-8.1	24	6.95 ± 0.37	6.4-7.6	17	1.47 NS	38.08	2.66

Depth	6.62 ± 0.39	6-7.6	24	6.2 ± 0.3	5.7-7	17	3.89***	38.8	6.34
Tarsus	41.1 ± 1.01	38.9-42.6	24	39.37 ± 1.3	36.9-41.5	17	4.59***	28.95	4.21
Wing	124.1 ± 3.1	117.3-128.5	24	115.8 ± 2.2	110-119	17	9.91***	38.99	6.69

Table 2.2 Accuracy in assigning sex of Floreana mockingbirds using a discriminant function analysis, denoted by Wilks' Lambda (ƛ) using single variables and combined functions of the variables.

		% correct			**% jack-knifing**		
Variable	**ƛ**	**Female (17)**	**Male (24)**	**Overall**	**Female**	**Male**	**Overall**
Weight	0.78	0.58	0.83	0.71	0.59	0.75	0.68
Head	0.72	0.65	0.79	0.73	0.65	0.79	0.73
Width	0.95	0.41	0.83	0.66	0.41	0.83	0.66
Deep	0.74	0.82	0.75	0.78	0.82	0.75	0.78
Tarsus	0.63	0.65	0.88	0.77	0.64	0.88	0.78
Wing	0.31	1	0.96	0.98	1	0.95	0.98
Wing +weight	0.28	1	0.96	0.98	1	0.96	0.98
Wing +tarsus	0.29	1	0.96	0.98	1	0.96	0.98

Wing +all beak	0.29	1	0.96	0.98	0.94	0.88	0.9
All variables	0.51	1	0.96	0.98	0.94	0.92	0.93

Chapter 3

Understanding the demography of the Floreana mockingbird: a step ahead in the reintroduction process

Floreana mockingbird tending to its nest.

Auckland, September 2021

Enzo M. R. Reyes

3.1 UNDERSTANDING THE DEMOGRAPHY OF THE FLOREANA MOCKINGBIRD: A STEP AHEAD IN THE REINTRODUCTION PROCESS

3.1.1 Article impact statement

This paper provides the first demographic estimates of the two remnant populations of the Floreana mockingbird using standardized capture-mark-recapture methods and the implementation of environmental variables on survival parameters. Notably the study found that despite the loss of genetic diversity the populations both remain stable in the current conditions. The study also highlights that the survival of the Floreana mockingbird is highly influenced by precipitation as found in other Galápagos land-birds. The study suggests that prolongated drought associated with La Niña and climate change could threaten the viability and persistence of both populations in the future. These estimates will be critical to enable a future population viability analysis that will inform decision making around the urgency of the species' reintroduction to Floreana Island.

Key words: survival, capture-mark-recapture, Pradel survival, POPAN, CJS Survival, population growth, endangered species, Galápagos Islands.

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Enzo M. R. Reyes: School of Natural Sciences, Massey University, North shore Mail Centre, Private Bag 102904, Auckland, New Zealand. enzorreyesb@gmail.com

Rebecca M. Boys: School of Computational and Natural Sciences, Massey University, North shore Mail Centre, Private Bag 102904, Auckland, New Zealand.

Paul F. Doherty Jr: Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, United States of America.

Adam C. Smith: School of Natural Sciences, Massey University, North shore Mail Centre, Private Bag 102904, Auckland, New Zealand.

Dianne H. Brunton: School of Natural Sciences, Massey University, North shore Mail Centre, Private Bag 102904, Auckland, New Zealand.

Danny Rueda: Galápagos National Park Directorate. Puerto Ayora, Santa Cruz Island, Ecuador.

Christian Sevilla: Galápagos National Park Directorate. Puerto Ayora, Santa Cruz Island, Ecuador.

Luis Ortiz-Catedral: School of Natural Sciences, Massey University, North shore Mail Centre, Private Bag 102904, Auckland, New Zealand and World Parrot Trust, Glanmor House, Hayle Cornwall TR27 4HB, United Kingdom.

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3.1.3 ABSTRACT

Demographic parameters allow researchers and conservationists to plan different strategies that could help to improve the conservation status of endangered species. One of the main tools for planning the management of endangered species is population viability analysis (PVA), a tool widely used in conservation biology, but requires species-specific parameters that only can be obtained through long term capture-mark-recapture data. In this study, we assessed five years of capture-mark-recapture of the two remnant populations of the endangered Floreana mockingbird (*Mimus trifasciatus*) with the aim of estimating the vital rates of the populations. Overall, we found that males have a higher survival compared with females. Furthermore, survival and recruitment were associated with the amount of rainfall over the islets. Finally, we found that the Champion population seems to be stable despite evidence of inbreeding, and contrary to our hypothesis, the Gardner population was slightly decreasing. The results presented here represent the first robust demographic estimation since the rediscovery of the species and support the recategorization of the species to endangered. Moreover, the vital rates presented here can be used as a baseline for multiple PVAs helping the decision-making process of the mockingbirds' reintroduction.

3.2 INTRODUCTION

In the era of the sixth mass extinction (Barnosky *et al*., 2011) understanding the demography, viability, and extinction risk of populations is an essential milestone for conservation planning of endangered species (Volis & Deng, 2020). In conservation, one of the main tools for the recovery of small populations and endangered species is translocations (Scott & Carpenter, 1987). Translocations is a key management strategy that involves the movement of living organisms to ensure their persistence from one area with a free release in another (IUCN, 1987). The success of translocations depends on several factors including the number of individuals released, knowledge of species ecology, logistical issues, and accurate species modelling (Bubac, Johnson, Fox, & Cullingham, 2019; Fischer & Lindenmayer, 2000; Knight, 2012; Morris, Brook, Moseby, & Johnson, 2021; Smeraldo *et al*., 2017). Population viability analysis (PVA) modelling has been used in several species and in different scenarios of translocations, either before or after the process to assess outcomes such as the persistence of the population without management (Cremona, Crowther, & Webb, 2017), potential consequences associated with the translocations (Verdon, Mitchell, & Clarke, 2021), movement strategy (Johnson & Greenwood, 2020) and consequences of genetic and behavioural factors (Keighley, Haslett, Zdenek, & Heinsohn, 2021). Although useful, PVA requires accurate species-specific demographic parameters, especially survival rates to create robust and realistic modelling (Akçakaya, 2000; Akçakaya & Sjögren-Gulve, 2000). However, species-specific demographic rates (fecundity and survival) and population abundance are lacking for many species. These parameters can be obtained through the use of systematic methods and long-term studies using capture-mark-recapture models (CMR) or distance sampling methods (Lebreton, Burnham, Clobert, & Anderson, 1992; Marshall, Diefenbach, Wood, & Cooper, 2004). CMR models are tools that have been widely used in demographic studies across species to assess the influence of biotic and abiotic factors on survival rates (Rockwell *et al*., 2017), diseases (Lachish, Jones, & McCallum, 2007) and anthropogenic impacts (López-Roig & Serra-Cobo, 2014). Further, in some cases, CMR can replace a basic PVA using specific models by estimating the population growth rate (Pradel, 1996).

The Floreana mockingbird (*Mimus trifasciatus*) is one of the most threatened species in the Galápagos Islands and has one of the most restricted distributions in the world (Ortiz-Catedral, Sevilla, Young, & Rueda, 2016). The species was distributed across the lowlands of Floreana Island until 1880 and then disappeared because of the introduction of invasive rats (Curry, 1986). The species now survives in two predator-free satellite islets (Champion and Gardner-by-Floreana) on the coast of Floreana Island. There is no gene flow between the populations, separated by 14km stretch of water, causing genetic and cultural divergence between populations (Hoeck, Keller, Beaumont, *et al.*, 2010; Hoeck, Keller, Bollmer, & Parker, 2010) and Chapter 4. For example, the smaller population on Champion has lost 39% of its expected heterozygosity due to genetic drift during the last century (Hoeck, Keller, Beaumont, *et al.*, 2010). Although, the loss of unique alleles that could create susceptibility to diseases and pathogens is a common trend in small populations (Frankham, 1995; Smith, Acevedo-Whitehouse, & Pedersen, 2009), in the Floreana mockingbird this has not yet occurred (Hoeck & Keller, 2012). Currently, the species inhabit an estimated of less than 1% of its original distribution (Wiedenfeld, 2003) and is a target for reintroduction attempts through the Floreana Island restoration project (Ortiz-Catedral, 2018). However, several aspects of the biology and ecology have yet to be studied in detail, including accurate estimates of demographic parameters which are required to assess the success of reintroduction attempts.

Only ten assessments of the whole Floreana mockingbird population have been conducted since 1906, with the first bird counts by Gifford (1919) to the summarized five years of censuses from Jiménez-Uzcáteui *et al.* (2011). Despite the proposed census methodology by Hoeck (2010), there is a disconcerting lack of consensus between methods, with most assessments only carried out for one of the two populations (Grant, Curry, & Grant, 2000;

Jiménez-Uzcátegui *et al.*, 2011). These methodological differences make data comparison complex and hinder any assessment of the demographic trajectory of the Floreana mockingbird population. Further, no aspects of its ecology and environmental factors have been considered in most of the censuses. Previous studies on other Galápagos land-birds have shown that demography is affected by precipitation, likely due to the role of rainfall as the primary factor in determining food-resource levels in the Galápagos environment (Grant & Boag, 1980). The seasonal environment of the Galápagos Islands is influenced by stochastic events such as El Niño and La Niña, that can affect the demographic trajectory of bird populations. Such effects have been recorded as impacting seabirds' survival during El Niño years (Vargas *et al.*, 2007) and involved in a population decline in land-birds during the unusual drought conditions of La Niña (Curry & Grant, 1989; Grant, 1985). Aside from the mortality caused by food shortage associated with prolonged droughts, Galápagos mockingbirds are also exposed to epizootic events related to environmental variation that produces high mortality (Curry, 1985). Another recent threat is the new invasion of the parasitic fly *Philornis downsi*, that has had a severe impact on the reproduction of most land-birds and in the recovery of critically endangered bird populations in the Galápagos (Fessl *et al.*, 2010; O'Connor, Sulloway, Robertson, & Kleindorfer, 2010). Although the impact of *P. downsi* on other Galápagos mockingbirds has not been as severe as in Darwin's finches (Knutie *et al.*, 2016), the effect that this parasitic fly will have on Floreana mockingbirds has not been assessed in detail yet (Ortiz-Catedral, *et al.* 2017). In the current predator-free environment, these drivers, along with possible effects from reduced genetic diversity because of inbreeding (Hoeck, Keller, Beaumont, *et al.*, 2010), are the main threats to the species. In this study, we estimated a variety of demographic parameters (survival, recruitment, population size and population growth rate) and population structure parameters (sex ratio and density) of the Floreana mockingbird using long term banding data. We hypothesized that survival would be influenced by sex and rainfall in both populations. Furthermore, for the small Champion, we hypothesised that the population growth will show a declining trend because of habitat saturation and inbreeding depression, whilst for the larger Gardner-by-Floreana, we expect a stable population.

3.3 METHODOLOGY

3.3.1 Study site

This study took place on the islets of Champion (90° 23’100’’W 01° 14’240’’S) and Gardner-by-Floreana (90°17’700’’W 01°19’969’’S) located in the northern part of Floreana Island-Galápagos Archipelago (Fig. 3.1). Champion is a circular islet of approximately 400 m in diameter and 9.4 ha in area; it is a crater that emerged from the seafloor whose maximum elevation is 46 m above sea level and is located 800 m from the coastline of Floreana Island (Grant, Curry, *et al.*, 2000). Because of the small size and accessibility, the study area covers the entire islet. Gardner-by-Floreana (hereafter Gardner) is a 76.5 ha islet located 8 km from the coast of Floreana; it is a large volcanic cone that has partially sunk creating an islet covered by cliffs of 50 to 100 m, and reaching an elevation of 210 m above the sea level. The islet has a 100 m high plateau of approximately 12 ha, located in the eastern part of the islet (Jiménez-Uzcátegui *et al.*, 2011), due to the complex accessibility, data for this study were only collected at this plateau.

3.3.2 Data Collection

A banding program of Floreana mockingbird was established in 2006 and continues to 2019 with over 400 individually marked birds on both Champion and Gardner. On

Champion, all individuals were banded as yearlings and the whole population is banded on the island. On Gardner birds were mostly banded as adults with a few banded as fledglings. Mockingbirds were captured in a wire cage trap with a lure and banded with one metal numbered band and a combination of one to three colour bands (New Zealand bird banding Scheme). To identify possible immigration between islets, Champion birds were banded on the left leg while Gardner birds were banded on the right leg. The age of the bird was categorized as adults or juveniles (yearlings) based on the plumage pattern (Curry & Grant, 1989). Floreana mockingbirds are not sexually dimorphic based on the plumage patterns, but males and females vary slightly in body size with males being larger than females (Hoeck, 2010). Sex was determined using a wing criterion where birds with wing chord equal to or over 19.5 were considered males (Chapter 2). Despite yearly monitoring, the sampling effort and month of sampling varied from year to year. To minimize capture heterogeneity, we reduced our dataset to a five-years from 2010 through 2016 (missing 2013) where the sampling effort was similar. Moreover, we focus on the months of November through February corresponding to the wet season along the Equator and the beginning of the breeding season of the Floreana mockingbird (Curry, 1985).

3.3.3 Mark-recapture modelling

Because of the non-dispersal between the populations, genetic differences (Hoeck, Keller, Beaumont, *et al.*, 2010; Hoeck, Keller, Bollmer, *et al.*, 2010), sampling methodology and intrapopulation dispersal, Capture-mark-recapture (CMR) models were applied to each population with population-specific demographic parameters of interest. Goodness of Fit (GOF) tests were carried out on the most general data structure for each population before CMR modelling. Closure of the populations was tested using the program *CloseTest*

(Stanley & Burnham, 1999), whilst transience and trap dependency were assessed using Test2 and Test3 respectively in Program *UCARE* (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) under the fully-time dependant Cormack-Jolly-Seber model (CJS) assumption. CMR models were fitted using program *MARK* (White & Burnham, 1999) to estimate demographic parameters of interest. Model selection was based on the Akaike information criterion or the quasi-likelihood criterion (QAICc,) (Anderson, Burnham, & White, 1994; Burnham & Anderson, 2004). Overdispersion ($\hat{c}$) was applied to CMR models where $\hat{c} > 1$ was found. In cases of under-dispersion ($\hat{c} < 1$), $\hat{c} = 1$ were applied following Cooch and White (2019). Models with ΔAICc <2 were considered to have support from the data and were used to estimate parameters.

3.3.4 Champion population

Apparent survival. - We estimated the apparent survival probability of the birds using the live recapture models (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965). This model estimates two parameters: apparent survival (Φ) where emigration is assumed to be permanent and confounded with mortality, and recapture probability (p) by conditioning in marked individuals. Individual capture histories were grouped by year (missing 2013) and sex (males and females). The missing year was modelled using the intervals arrangement in *MARK* before fitting the models. We investigate the effects of sex and time in Champion where the entire population is banded. Since surveys were conducted across the entire island each year and previous studies reported population isolation, we suggest that any new bird appearing in consecutive years belongs to a yearling from the previous year. Additionally, we assume that any bird disappearing completely from the population through the study period is probably likely to be linked to the death of the birds rather than emigration, because birds banded in one population have never been found in the other population to date. Based on previous studies we expected that environmental variation may affect the survival and capture probability of the birds. Rainfall data from the Galápagos Islands was extracted from the averaging rainfall of Charles Darwin Research meteorological station (www.darwinfoundation.org) located in the lowlands of Santa Cruz Island (Fig. 3.1). Precipitation was added as a real population covariate in the design matrix of *MARK*, in a full-time dependant model and expressed as averaging rainfall during each year in the study. Both parameters, apparent survival (Φ) and capture probability (p) were modelled as constant, sex dependant, time-varying or varying as a function of the population level covariate precipitation, and as a combined effect of sex and precipitation.

Recruitment and Population Growth. -We assessed the population growth rate using the Pradel survival and recruitment models (Pradel, 1996). In this model the realized population growth (λ) can be calculated as a derived parameter of recruitment (f) and represents the observed change in population and does not assume constant ergodic conditions, or stable age distribution. We estimated the average growth rate throughout the study by calculating the geometric mean of λ through the derived estimates of $\ln(\lambda)$. As Pradel models do not allow for "age effects" we pooled all our individuals as adults for the analysis. We expect that recruitment values on Champion are due to the survival of juveniles since there is no immigration between islands reported yet (Grant, 1983). We modelled the parameters of apparent survival, capture probability and f as constant, time-varying, affected by sex and with average rainfall as a population level covariate. We also examined whether the interaction between sex and rainfall affected these parameters. Finally, we did not estimate population abundance on Champion since yearly abundance can be estimated through individual counts.

3.3.5 Gardner population

Apparent survival, probability of entrance and abundance. - Since sampling on Gardner can only be carried out on a small section of the islet, only a proportion of the population is banded. We estimated the population parameters on this islet using the *POPAN* model (Schwarz & Arnason, 1996). *POPAN* assumes the presence of a super-population, enabling estimation of abundance including those individuals outside the study area, and for movement into the study area. In this model, we calculated the probability that a mockingbird from the super-population entered the study area between years t and t+1; this probability of entry (*pent*) can be interpreted as adult immigration and juvenile recruitment into the adult class. We did not include age effects in our model because of the lack of age information when individuals were banded. Apparent survival (Φ), capture probability (p) and probability of entry (*pent*) were modelled as constant, time-varying and with sex. The values of average precipitation were also modelled as a population level covariate and applied to all modelled parameters.

Recruitment and Population Growth. - We used the same approach described above to estimate the recruitment probability and the realized population growth in Gardner. Recruitment in the study area is expected to be a combination of new-hatched and immigrants from other parts of the island

3.3.6 Sex ratio, density, longevity, and lifespan

We used the estimates of population size in both populations to calculate the tertiary sex ratio of the population expressed as the percentage of males among adults of known sex. The population density was calculated by dividing the population size by the area (ha) of the islets. Sex ratio and density are reported as the average of the study duration.

Longevity was calculated by direct observation of banded individuals and lifespan was calculated as 1/-ln(s) where s is the mean survival of the population (Cooch & White, 2017).

3.4 RESULTS

As expected, the results of *CloseTest* indicated that both populations are open (Champion: Chi^2 = 145.32, df = 11, $p \leq 0.001$; Gardner: Chi^2 = 420.97, df = 11, $p \leq 0.001$). GOF sum of Test 2 and Test 3 in program *UCARE* showed minimal overdispersion ($\hat{c}$) in the datasets (Champion: 0.74, Chi^2 = 14.1058, *df*= 19, p= 0.77; Gardner: 1.02, Chi^2 = 22.3756, *df*= 22, p= 0.44) . Overdispersion value of 1.02 was applied to Gardner models in program MARK, whilst Champion was left at the default of 1.0 following Cooch and white (2019). Neither dataset showed significant effects of transience (Champion: p = 0.45; Gardner p = 0.54) or trap-dependency (Champion: p = 0.66; Gardner: p = 0.19).

3.4.1 Survival, recruitment, and population growth in Champion

We compared 44 models for the survival on Champion and the models that best fitted our data were *Φ(sex+rain)p(sex+rain)* and *Φ(sex+rain)p(sex)* (Table 3.1). Both models fit the data well (Chi^2= 2.716, *df*= 1, p= 0.09). So, we averaged these two models to obtain survival estimates (Fig. 3.2 a). Survival estimates for males were higher (0.86 ±0.04 SE) than for females (0.74 ±0.08 SE) over the study period.

We compared 24 models of population recruitment and obtained three models with a ΔAICc under 2 (Table 3.2). The best model was *Φ(sex+rain) p(sex) f(rain),* although the competing models *Φ(sex+rain) p(sex+rain) f(rain)* and *Φ(sex+rain) p(sex) f(sex+rain)* also fitted the data well (Chi^2= 1.296, *df*= 1, p= 0.25; Chi^2= 0.95, *df*= 1, p= 0.33). We averaged these three models to obtain recruitment estimates. In which recruitment (*f*) seems to be higher during low rain years (Table 3.5), and similar for females (0.19, ± 0.08 SE) and males (0.18, ± 0.07 SE). The geometric average population growth during the study was 1.05 which indicate a slow increase of the population during the study. Population growth remained relatively stable throughout the study period (Fig 3.3).

3.4.2 Survival, abundance, recruitment, and population growth in Gardner

From the 31 models explored for suvirval and abundance, those with rainfall and sex on survival and pent were the best candidates (Table 3.3). The models that best fit the data had survival parameters modelled with rainfall and sex, also had a probability of entry modelled with rainfall and sex. We averaged the first two models with ΔAICc under 2 *p(sex+time) Φ(sex+rain) b(sex+rain)* and *p(time)Φ(sex+rain) b(sex+rain)* that fitted well our data (Chi^2= 2.474, *df*= 1, p= 0.12). Mean survival in Gardner was slightly higher for males (0.76, ± 0.04 SE) than for females (0.66, ± 0.06 SE) and influenced by the rainfall pattern (Fig. 3.2 b; Fig 3.1). PENT was higher for females (0.1, ± 0.03 SE) than for males (0.08, ± 0.02 SE) and higher for both sexes during years of low rain (Fig. 3.4). The abundance (Table 3.5) in the study area seems to have been decreased after 2012. Overall males seem to be more abundant than females (Fig. 3.5). Recruitment was higher in low rain periods (Table 3.5) and was higher for females (0.26, ±0.1 SE) than for males (0.15, ± 0.05 SE). The geometric average population growth during the study was 0.88 which indicate a slight decrease in population growth throughout the study. Population growth by encounter occasions seems to follow the same pattern that recruitment with an increment of the population during low rain years (Fig 3.3).

3.4.3 Sex ratio, density, longevity, and lifespan

In Champion, the sex ratio of males was variable from 60% in 2010 to 48% in 2011 (Table 3.6). Overall sex ratio was biased towards males (57%) during our study period. Density was calculated at 3.3 individuals/ha. Lifespan for individuals on Champion was estimated at 5.73 years.

Sex ratio in males of Gardner varied from 61.32% in 2010 to 58.13% in 2016 (Table 3.6). Overall sex ratio was male-biased with more males (61%) than females (39%). Density in Gardner was calculated by extrapolating the average 159.38 (± 0.33 SE) individuals from the 12-ha study area during our study to the total area of Gardner (76.5 ha) resulting in 13.25 individuals/ha. The lifespan for individuals on Gardner was estimated at 2.92 years. Furthermore, outside the period of study, we found that Floreana mockingbirds are long-lived species. Three individuals (two on Champion and one in Gardner) captured as a yearling on 2006 were last time seen in 2016 having lived at least 10 years.

3.5 DISCUSSION

3.5.1 Survival

Adult survival is the more important vital rate when modelling population viability analysis (PVA), especially when modelling cooperative breeding bird systems (Mortensen & Reed, 2016). As expected, survival of the species is highly influenced by the amount of rainfall over the islets. Survival in both populations decreased during years with low rain. Grant *et al*. (2000) found the same pattern of high mortality during the low rain years of 1988 and 1989. Similar results have been found for the Galápagos mockingbird (*Mimus parvulus*) with low rates of reproduction and high adult mortality (Curry, 1985; Curry & Grant, 1989). Similar to other landbirds in the Galápagos (Grant,

Grant, Keller, & Petren, 2000; Wiedenfeld & Jiménez-Uzcátegui, 2008; Wingfield *et al.*, 2018), Floreana mockingbirds survival rates seem to be highly sensitive during periods of drought expected to increase in frequency and intensity globally due to climate change (Cai, Santoso, *et al.*, 2015; Cai, Wang, *et al.*, 2015). On the other hand, the increasing survival rates during the last encounter occasion seems to be related to an increase in rain associated with the strong El Niño during 2015-2016 (Santoso, Mcphaden, & Cai, 2017). Heavy rains during El Niño conditions create a bonanza of food resources that favour reproduction and increase the population abundance of many landbirds in the Galápagos (Gibbs & Grant, 1987; Grant & Grant, 1987).

Among the small population of Champion, survival seems to be stable across the years. Our mean of both sexes combined during the study period of 0.86 (±0.06 SE) is similar to the mean of both sexes combined of 0.81 from 1986 to 1988 reported by Grant *et al.* (2000). Nevertheless, these two survival estimates are higher than Gardner population (0.71 ± 0.05 SE). Unfortunately, there are not any previous estimations of survival for Gardner to which our results could be compared. The difference in the survival between the two populations could be explained by several factors, such as small differences in the rainfall between islands because of island orography (Reed, 1980), habitat structure (Curry, 1986; Ascencio (in preparation) & Appendix 1), body size between populations (Chapter 3), different local densities (see density below), temporary presence of invasive avian species (Jiménez-Uzcátegui *et al.*, 2011), the difference in density and predation by the native Galápagos short-eared owl (*Asio flameus galapagoensis*), a species present in Floreana that can fly between islands (Schulwitz *et al.*, 2018) and predate on mockingbirds (Curry & Grant, 1989). Further differences include the impact by predation of migratory Peregrine falcon (*Falco peregrinus*) (Reyes and Ortiz-Catedral pers. obs.)

and/or differences in the prevalence of parasites, pathogens and epizootic events between islands (Curry, 1985; Deem, Parker, Merkel, Cruz, & Hoeck, 2011; Grant, Curry, *et al.*, 2000; Ortiz-Catedral *et al.*, 2016). Nevertheless, the differences in the survival among sexes could be explained by the fact that males are larger than females (Chapter 2) and because dispersal in cooperative breeding mockingbirds is female-biased (Payevsky, 2021). Females disperse earlier and further than males, increasing the probability of mortality by group rejection and starvation (Curry & Grant, 1989; Eikenaar, Richardson, Brouwer, & Komdeur, 2008; Temple, Hoffman, & Amos, 2006). We rejected the possibility that survival by sex is caused by effects of a sex-biased inbreeding effect as happens with other endangered species (Brekke, Bennett, Wang, Pettorelli, & Ewen, 2010) as the same pattern of female survival is presented in both populations that harbour different levels of genetic diversity (Hoeck, Keller, Beaumont, *et al.*, 2010).

Overall, our survival estimates for Champion and Gardner were higher than for the other two conspecific Galápagos mockingbirds for which survival data is available. For the Galápagos mockingbird (*M. parvulus)* in Genovesa Island, Curry and Grant (1989) estimated the survival as 0.61 during a 10-years period. Additionally, for the Española mockingbird (*M. macdonaldi*) the average survival combining males and females was estimated at 0.69 for a four years period (Von Lippke, 2008). Outside the Galápagos, our estimates are higher than for other members of the Mimidae family. In the case of the tropical mockingbird (*M. gilvus),* another cooperative breeding bird, the annual adult survival rate was estimated at 0.77 for four years. (de Araujo, 2016). Similarly, another endangered cooperative breeder Santa Lucia Thrasher (*Ramphocinclus sanctaeluciae*) had an adult survival estimation of 0.69 during a three-year study in Santa Lucia Island (Mortensen, 2009), although Temple (2006) found for the same population an adult survival estimates of 0.87, for a period higher than our estimate. Finally, for the critically endangered Socorro mockingbird (*Mimoides graysoni*), adult survival was estimated at 0.54 during a short-term study (Martínez-Gómez & Curry, 1996). Further, outside of the Mimidae family, our estimates were also high compared with another endangered cooperative breeding bird like the Micronesian kingfisher (*Todiramphus cinnamominus*) with a survival estimation of 0.58 for adult birds (Kesler & Haig, 2007) similar to the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*) (Brouwer, Richardson, Eikenaar, & Komdeur, 2006). However, the survival of the Floreana mockingbirds could be conditioned to the group structure and sociality (Von Lippke, 2008). Our high survival estimates might be explained by the fact that the species live in a pristine, relatively invasive predator-free environment in which the habitat has not been affected by the introduction of invasive browsers. Finally, we feel confident of our results because the open habitat (Appendix 1) and high group philopatry and catchability of Floreana mockingbirds, factors which decrease the probability of error or bias in the estimation of the survival of the species (de Araujo, 2016). Additionally, because of the closed nature of Champion population, our estimates of survival are not confounded with dispersal, which is not the case for Gardner in which survival was calculated with dispersal-migration as the probability of entrance in the study population (Fig. 3.4).

3.5.2 Recruitment, Population growth and Population size.

In this study, we define annual recruitment as the production of juvenile birds that survive to be incorporated in the adult class in a given year. Annual recruitment in both islands follows the opposite pattern of survival, with high recruitment of individuals during years with low rain (Table 3.5). Recruitment estimates were high when the mortality rate was high as there are more spaces available in the territories that can be filled by new individuals since the low densities enable new birds to obtain a space for breeding (Curry & Grant, 1989). Overall, annual average recruitment for both populations (0.19 for Champion and 0.07 for Gardner) was lower than the average recruitment in other cooperative breeders. The recruitment rate in the Santa Lucia thrasher (*R. sanctaeluciae*) was estimated at 0.43 during 2003 and 2004 (Temple, 2006), and 0.60 estimated for the Seychelles warbler in a 20-year CMR study (Brouwer, Richardson, & Komdeur, 2012). In this study, average annual mortality for Champion and Gardner were calculated at 0.16 and 0.29 respectively. To prevent the decline of the populations', recruitment rates should be equal or greater than the mortality threshold of 0.16 for Champion and 0.29 for Gardner. Our results for recruitment match our estimates of population growth. The Champion population seems to be stable and slightly growing. While for Gardner, due to the low rate of recruitment and high mortality, the population seems to be decreasing by approximately 9% over each of the study years (Fig. 3.3).

Population size on Champion can be easily calculated by counting the number of birds banded as the entire population has been marked. During our study, the average number of birds present in Champion was 31 individuals (± 2.37 SE). On the other hand, Gardner population size has been estimated using transects and point counts which has resulted in different estimations across the years, and an underestimation of the population size with a fluctuation between 85 to 225 individuals (Jiménez-Uzcátegui *et al.*, 2011). During the period of this study, program Mark estimates the average (males and females pooled) population size of our study area (12 ha) as 159 individuals (± 0.34 SE). Based on these results, we estimate the population size of Gardner (76.5 ha) to be 1014 individuals. Our estimates support the reclassification of 2017 in which the Floreana mockingbird was upgraded from critically endangered to the endangered category of the IUCN (BirdLife International 2021).

Accurate estimates of population size are an important parameter to understand the population dynamics, set conservation milestones for endangered species (Mace *et al.*, 2008), and it is one of the main aspects used when population modelling is performed (Oro, Aguilar, Igual, & Louzao, 2004). Underestimation and overestimation of population size are common problems that can result in a misinterpretation of the probability of extinction in endangered species, especially in short term monitoring (Reed, O'Grady, Brook, Ballou, & Frankham, 2003). Methods for the estimation of population size can vary in accuracy depending on factors like species and habitat (Casagrande & Beissinger, 1997; Schwarz & Seber, 1999). In this study, we believe our estimates from CMR methods are very reliable as the assumptions of the method were accounted for because mockingbirds are relatively easy to catch, and the features of the habitat allow us a high rate of individual encounter probability (not shown in this study).

3.5.3 Population structure

Our estimates of sex ratio differ from the estimates of Curry (1989) where females predominate on Champion with exception of 1983 when males overtook females. On Gardner, our results follow the same pattern found by Deem *et al.* (2011), which despite the small sample size, found that males outnumbered females by 59%. Nevertheless, the sex ratio in critically endangered birds is strong biased towards males (Payevsky, 2021) and can vary between populations (Curry, 1989; Deem *et al.*, 2011; Von Lippke, 2008) and between times because the influence of environmental factors (Curry & Grant, 1989).

On Champion, densities reported by Curry (1989) and Grant *et al.* (2000) are similar to the densities found in this study, which implies that the population hasn't changed much during the last 32 years. Meanwhile for Gardner average population density is four times denser than for Champion. Similarly, high values of densities have been found for the Española mockingbird (*M. macdonaldi*) when it occupies coastal habitat (Curry, 1989). The high densities of mockingbirds on Gardner found in this study could explain the lower survival compared with Champion. In another cooperative breeding bird (Seychelles warbler) there is evidence that high densities influence negatively the survival of individuals (Brouwer *et al.*, 2006). Density estimates of mockingbirds for both populations are higher than for the critically endangered Santa Lucia Thrasher (*R. sanctaeluciae*) which is suggested to be a different species of the white-breasted thrasher (*R. brachyusus*) (DaCosta *et al.*, 2019). In which estimates are calculated between 1.79 to 2.71 individuals/ha before the clearance of habitat by a touristic development in Santa Lucia Island (Temple, 2006; Young *et al.*, 2010).

The oldest bird recorded from the two populations was estimated to be 10 years. Similar longevity has been reported for the Galápagos mockingbird (*M. parvulus*) with individuals living over the seven years and expected to live until 12 years (Curry & Grant, 1989). These values seem to be aligned with the average of other neotropical passerines where CMR studies have been applied (Scholer, Merkord, Londoño, & Jankowski, 2018; Silva-Jr, Kajiki, Diniz, & Kanegae, 2020). Nevertheless, due to the differences in survival and densities between islands, lifespan differs between populations, with birds on Gardner living almost half as long as the birds living on Champion.

3.5.4 Implications for conservation and reintroductions

For the first time, we calculated accurate estimations of the demographic and vital rates for both populations of the Floreana mockingbird. We achieved this by using a standardized methodology and robust mathematical models. With the vital rates generated by this study, the population trend of the species suggested as a “research needed” by the IUCN can be calculated using models of PVA. With which adequate methods of harvesting for the reintroduction, and population persistence (with and without conservation actions) can be calculated. The population, in general, seems to be stable, with a slight decrease on Gardner that need to be investigated by the improvement of the monitoring strategy. Standardization of monitoring will allow the use of more detailed models of CMR such as the robust design or multistate models that will respond to answers related to migration, dispersal, and transition between social status. Moreover, Floreana mockingbirds live in a restricted habitat which makes them vulnerable to stochastic events such as prolonged droughts and epizootic events. Reintroduction of the species is advisable to ensure the persistence of the species via a third population on Floreana Island, before the impacts of climate change, particularly the increasing, intensity and frequency of droughts, as predicted by climate modelling.

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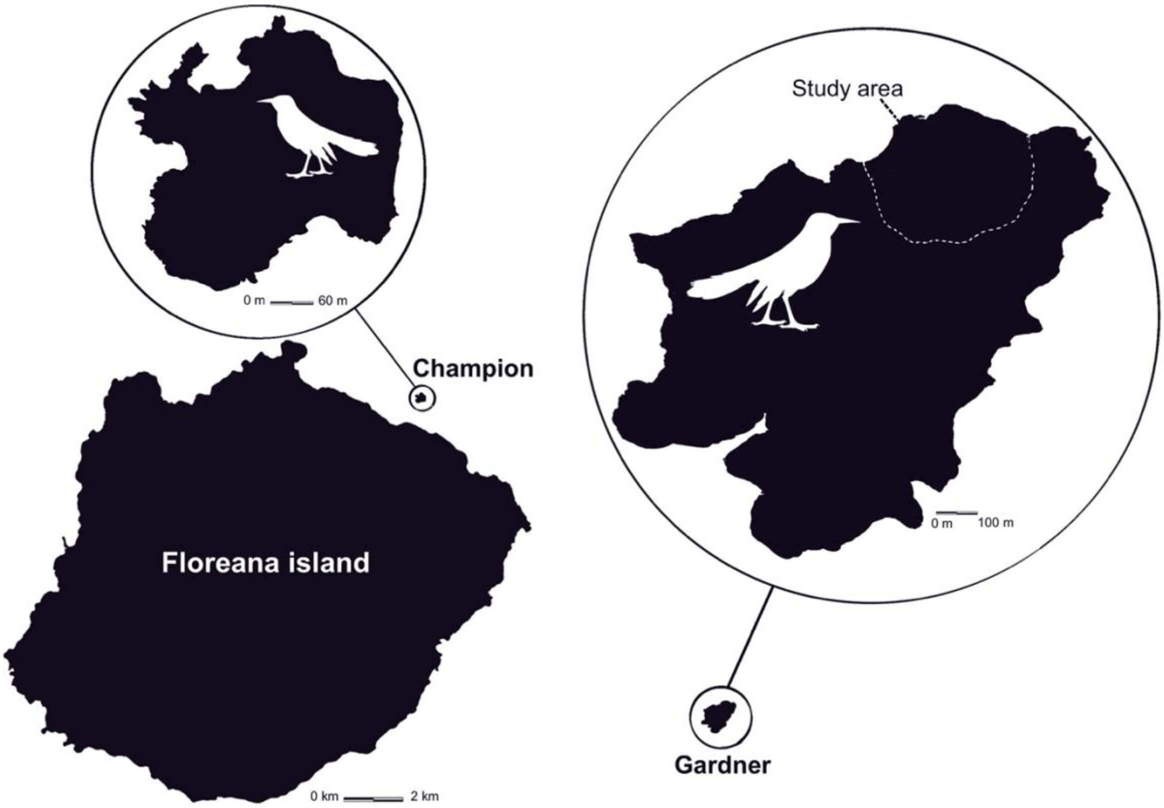

Figure 3.1 Location of the islets of Champion and Gardner. In Champion, Floreana mockingbird population is monitored in the whole islet due to the small size (8 ha). Meanwhile for Gardner the dotted area corresponds to the 12 ha plateau in the north of the islet.

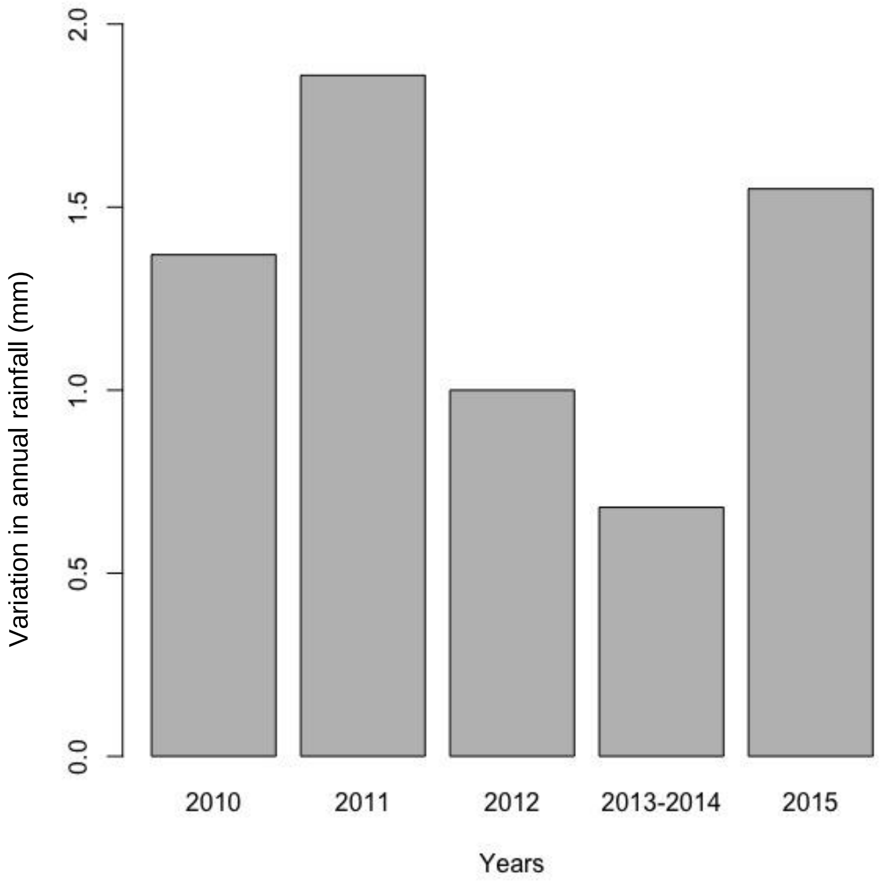

Figure 3.2 Annual averaging of the rainfall in the Galápagos Islands. Years 2013 and 2014 were averaged as one, to match the structure of the models in program MARK where 2013 event was missing. Data was obtained from Puerto Ayora meteorological station located ~ 60 Km north of the study area. Location was chosen from the only two available meteorological stations in the archipelago because proximity and habitat similarity.

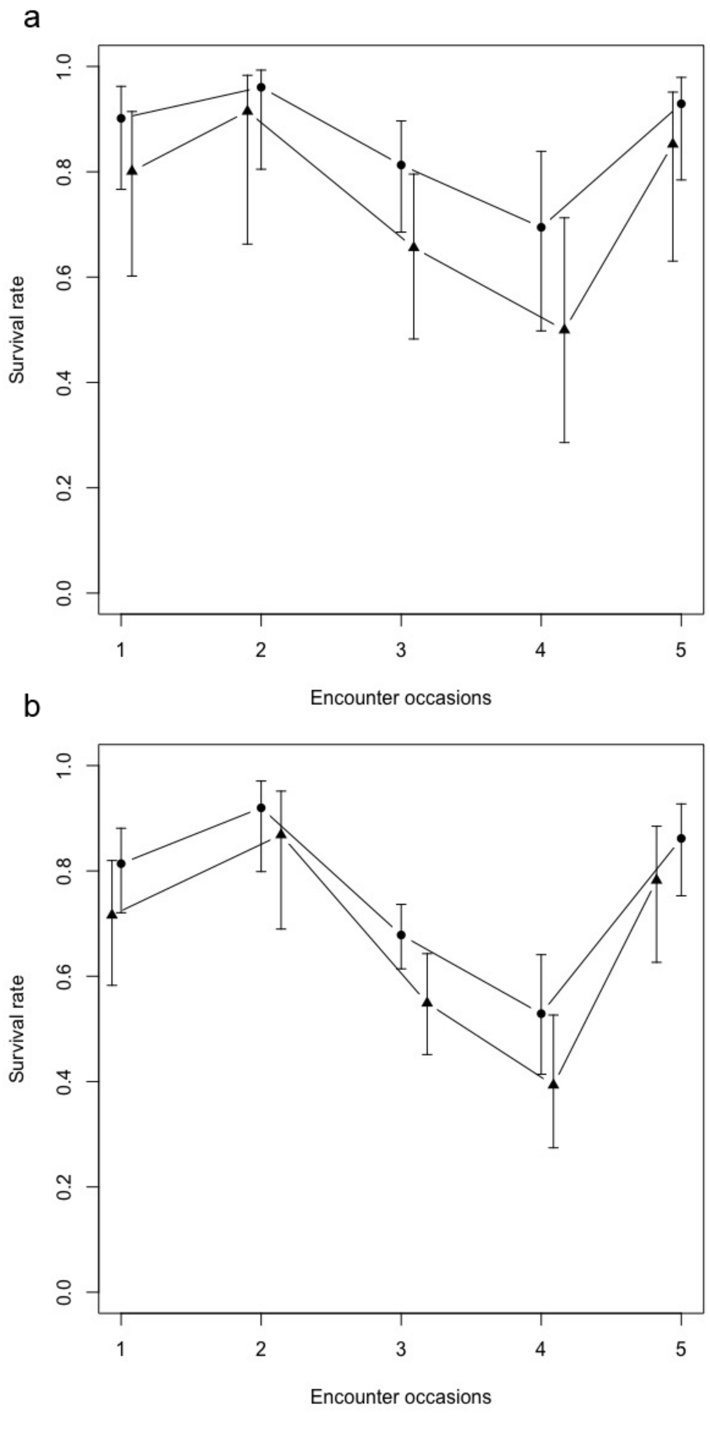

Figure 3.3 Survival estimates for the **a)** Champion and **b)** Gardner populations during the study period. Filled circles (●) show survival rate of males and filled triangles (▲) show the survival rate of females. Mean is shown ± 95% CI. Female estimates were jiggered moved in the x axis to avoid overlapping with male estimates.

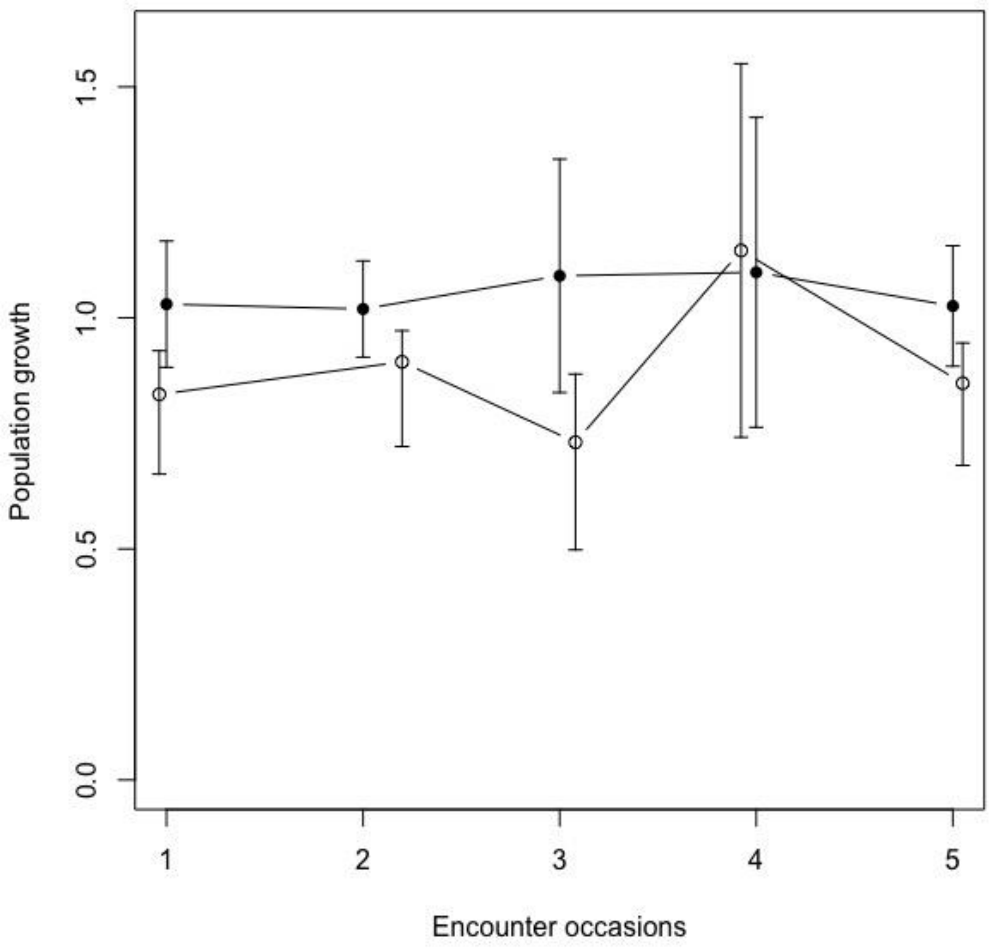

Figure 3.4 Average population growth of males and females pooled together in both populations. Filled circles (●) show the estimates of the realized population growth (λ) for Champion while empty circles (o) represent λ for Gardner population.

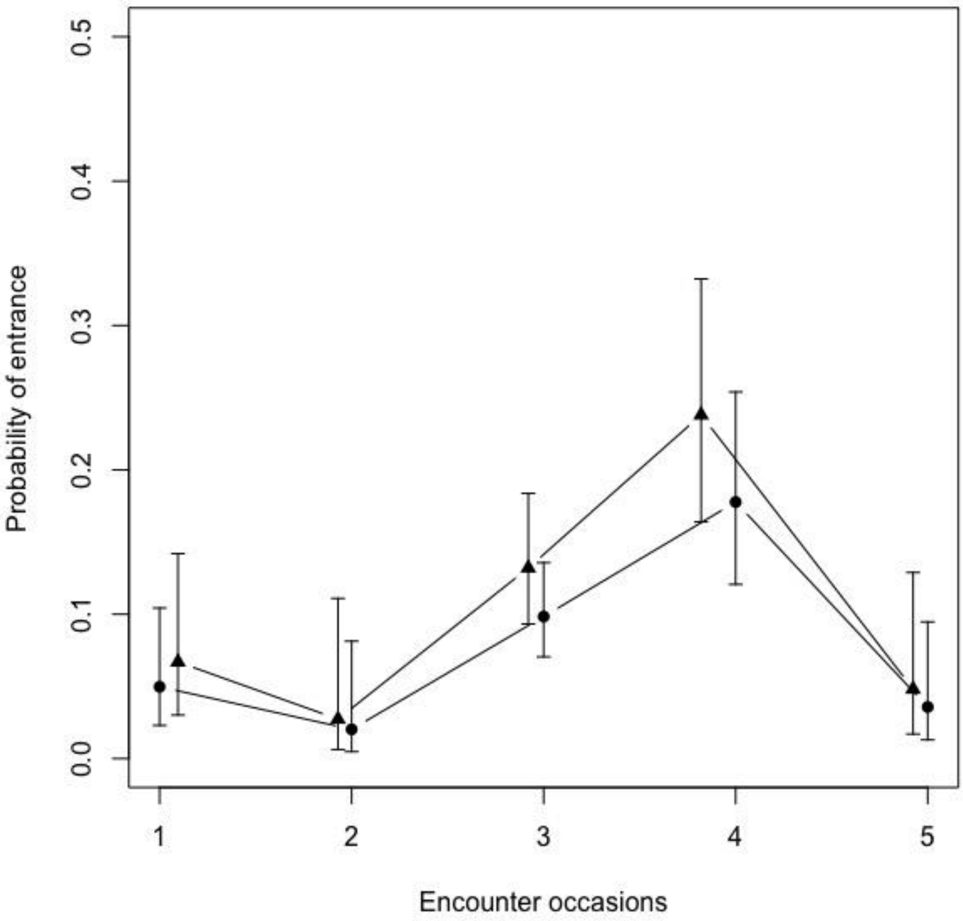

Figure 3.5 Probability of entrance from the Gardner superpopulation to the study area. Filled circles (●) show the probability of entrance rate of males and filled triangles (▲) show the probability of rate of females. Mean is shown ± 95% CI. Female estimates were jiggered in the x axis to avoid overlapping with male estimates.

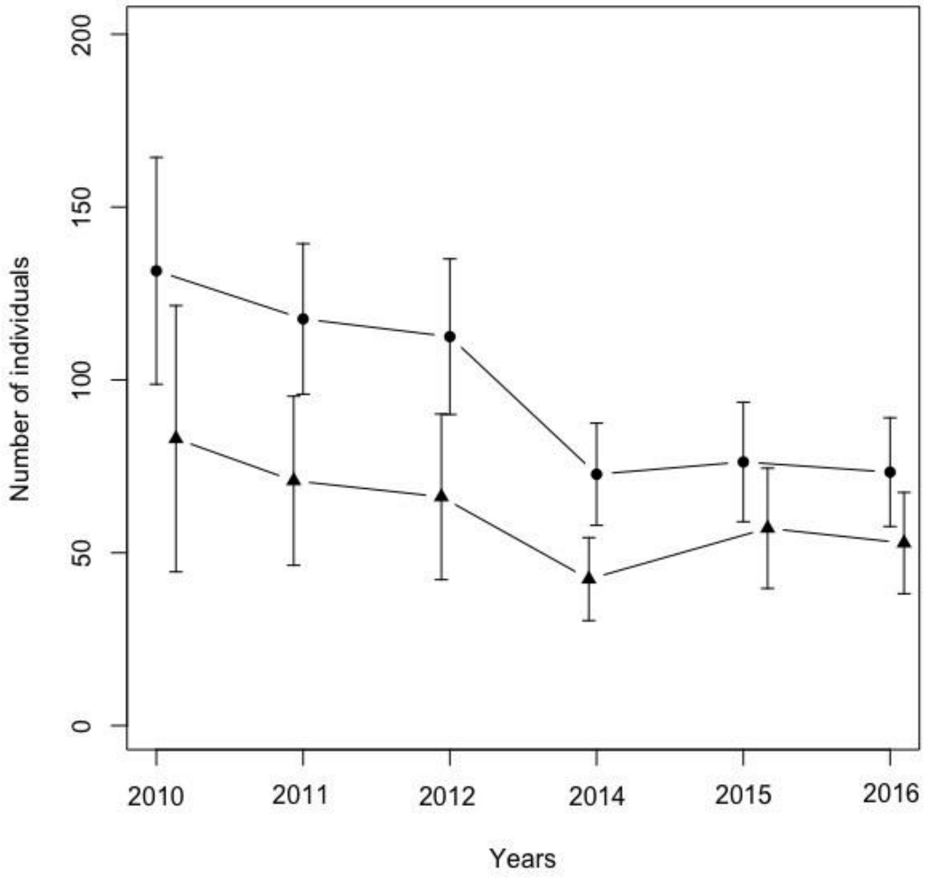

Figure 3.6 Number of individuals estimated on the Gardner study area during the study period. Filled circles (●) shows the estimates of males and filled triangles (▲) shows the estimates of females. Female estimates were jiggered in the x axis to avoid overlapping with male estimates. Error bars are ± 95% CI.

Table 3.1 Summary result of the sex structured CJS analysis of apparent survival and recapture rates for Champion population. Table includes the best nine models according to the AICc in addition to the global model, model 10 in the table.

Model no.	Model	AICc	*Δ*AICc	AICc Weight	np	Deviance
1	*Φ(sex+rain)p(sex+rain)*	283.20	0.00	0.36	6	92.25
2	*Φ(sex+rain)p(sex)*	283.75	0.55	0.27	5	94.97
3	*Φ(sex*rain)p(sex*rain)*	285.83	2.63	0.09	8	90.46
4	*Φ(sex*rain)p(sex)*	285.84	2.65	0.09	6	94.90
5	*Φ(rain)p(sex*time)*	286.38	3.18	0.07	12	81.79
6	*Φ(rain)p(rain)*	287.15	3.95	0.05	4	100.51
7	*Φ(sex+rain)p(sex*time)*	287.71	4.52	0.04	13	80.74
8	*Φ(sex*rain)p(sex*time)*	289.48	6.28	0.01	14	80.09
9	*Φ(sex)p(sex)*	291.69	8.49	0.01	4	105.04
10	*Φ(sex*time)p(sex*time)*	300.01	16.89	0.00	20	75.39

Table 3.2 Summary result of the sex structured Pradel survival and recruitment analysis of apparent survival and recapture rates for Champion population. Table includes the best nine models according to the AICc in addition to the global model, model 10 in the table.

Model no.	Model	AICc	*Δ*AICc	AICc Weight	np	Deviance
1	*Φ(sex+rain)p(sex)f(rain)*	561.65	0.00	0.35	7	95.20
2	*Φ(sex+rain)p(sex+rain)f(rain)*	562.54	0.89	0.23	8	93.90
3	*Φ(sex+rain)p(sex)f(sex+rain)*	562.88	1.22	0.19	8	94.24
4	*Φ(sex+rain)p(sex)f(sex+rain)*	563.63	1.99	0.13	9	92.79
5	*Φ(sex+rain)p(sex+rain)f(sex+rain)*	565.0.4	3.38	0.06	9	94.19
6	*Φ(sex+rain)p(sex)f(sex*rain)*	566.84	5.19	0.03	12	89.23
7	*Φ(time)p(sex)f(time)*	570.51	8.85	0.00	9	99.66
8	*Φ(time)p(sex)f(sex)*	572.54	10.89	0.00	11	97.21
9	*Φ(time)p(.)f(time)*	573.21	11.56	0.00	6	108.92
10	*Φ(sex*time)p(sex*time)f(sex*time)*	605.23	43.57	0.00	32	75.68

Table 3.3 Summary result of the sex structured *POPAN* analysis of apparent survival, recapture rates and probability of entrance in Gardner population. Table includes the best nine models according to the AICc in addition to the global model, model 10 in the table.

Model no.	Model	AICc	*Δ*AICc	AICc Weight	np	Deviance
1	*p(sex+time)Φ(sex+rain)pent(sex+rain)*	818.73	0.00	0.24	15	-869.03
2	*p(time)Φ(sex+rain)pent(sex+rain)*	819.08	0.35	0.20	14	-866.55
3	*p(time)Φ(sex+rain)pent(sex*rain)*	819.82	1.08	0.14	15	-867.95
4	*p(time)Φ(sex*rain)pent(sex+rain)*	819.95	1.22	0.13	15	-867.81
5	*p(time)Φ(sex*rain)pent(sex*rain)*	820.00	1.27	0.13	16	-869.88
6	*p(time)Φ(sex+rain)pent(time)*	820.88	2.15	0.08	14	-864.75
7	*p(time)Φ(sex+rain)pent(rain)*	821.62	2.90	0.06	13	-861.88
8	*p(rain)Φ(sex+rain)pent(sex+rain)*	824.69	5.96	0.01	10	-852.53
9	*p(sex*time)Φ(sex+rain)pent(sex+rain)*	828.21	9.47	0.00	20	-870.31
10	*p(sex*time)Φ(sex*time)pent(sex*time)*	850.74	32.00	0.00	34	-879.13

Table 3.4 Summary result of the sex structured Pradel survival and recruitment analysis of apparent survival and recapture rates for Gardner population. Table includes the best nine models according to the AICc in addition to the global model, model 10 in the table.

Model no.	Model	AICc	*Δ*AICc	AICc Weight	np	Deviance
1	*Φ(sex+rain)p(time+sex)f(sex+rain)*	1767.07	0.00	0.48	13	83.55
2	*Φ(sex+rain)p(time)f(sex+rain)*	1768.34	1.27	0.25	12	86.93
3	*Φ(sex+rain)p(time+sex)f(rain)*	1769.70	2.63	0.13	12	88.29
4	*Φ(sex*rain)p(time)f(sex+rain)*	1769.84	2.77	0.12	13	86.32
5	*Φ(sex*rain)p(rain)f(sex+rain)*	1776.01	8.94	0.01	9	100.87
6	*Φ(sex+rain)p(time*sex)f(sex*rain)*	1776.74	9.66	0.00	18	82.55
7	*Φ(sex+rain)p(rain)f(sex+rain)*	1777.44	10.37	0.00	8	104.37
8	*Φ(sex*rain)p(rain)f(sex*rain)*	1777.45	10.38	0.00	10	100.23
9	*Φ(sex+rain)p(sex+rain)f(sex+rain)*	1778.13	11.05	0.00	9	102.98
10	*Φ(sex*time)p(sex*time)f(sex*time)*	1786.26	19.19	0.00	25	76.75

Table 3.5 Average recruitment estimates of males and females (pooled) of both islands using Pradel survival and recruitment model in program *MARK*.

Occasions	Champion	SE	Gardner	SE
1 (2010-2011)	0.12	0.07	0.07	0.05
2 (2011-2012)	0.05	0.05	0.02	0.02
3 (2012-2014)	0.25	0.06	0.24	0.06
4 (2014-2015)	0.46	0.15	0.68	0.20
5 (2015-2016)	0.09	0.06	0.04	0.04

Table 3.6 Variation in sex ratio percentage during 2010 to 2016 (missing 2013) in both populations.

	Champion				Gardner			
Year	All birds	Males	Females	% sex ratio	All birds	Males	Females	% sex ratio
2010	25	15	10	60.00	214.55	131.56	82.99	61.32
2011	29	14	15	48.28	188.48	117.65	70.83	62.42
2012	36	19	17	52.78	178.69	112.52	66.18	62.97
2014	25	16	9	64.00	115.08	72.71	42.37	63.18
2015	39	23	16	58.97	133.35	76.27	57.08	57.19
2016	33	19	14	57.58	126.13	73.33	52.81	58.13
x̄±SE				56.9±2.28				60.9±1.05

Chapter 4

Drifting apart: cultural divergence and morphological variations of two remnant populations of the endangered Floreana mockingbird

Floreana mockingbird singing from a high cactus perch

Wellington, November 2021

Enzo M. R Reyes

4.1 DRIFTING APART: CULTURAL DIVERGENCE AND MORPHOLOGICAL VARIATIONS OF TWO REMNANT POPULATIONS OF THE ENDANGERED FLOREANA MOCKINGBIRD

Short title: Cultural and morphological divergence in the Floreana mockingbird

Enzo M. R. Reyes[1*], Michelle M. Roper[1], Dianne H. Brunton[1], , Christian Sevilla[2], Danny Rueda[2], Adam N. H. Smith[1] ,Luis Ortiz-Catedral[1]

[1]School of Natural Sciences, Massey University, North Shore Mail Centre, Private Bag 102904, Auckland, New Zealand.

[2]Galápagos National Park Directorate, Puerto Ayora, Galápagos, Ecuador.

corresponding author: enzorreyesb@gmail.com

4.2 ABSTRACT

Despite the importance on cultural (acoustic and behavioural) factors on wild populations and their possible consequences as a gene flow barrier and negative impacts on the success of reintroductions, the effects of cultural divergence have only recently been recognised within the context of conservation biology. Here, we investigate the extent, and potential impacts, of cultural divergence in two isolated populations of the Floreana mockingbird (*Mimus trifasciatus*), an endangered songbird of the Galápagos Islands. These populations are the focus of a current planned reintroduction to Floreana Island. We compared acoustic characteristics of the mockingbird's vocalisations and morphology of these two remnant populations and assessed the changes in vocalisations by comparing the acoustic characteristics of recordings from two time periods: 1962 and 2019. We found evidence for spatial and temporal differentiation in vocalisations between the two periods. Canonical analysis of principal coordinates (CAP) classified over 75% of the birds to the correct populations based on multivariate vocalisation measures. We also found significant differences in morphometrics between populations, with beak width being associated with variation in mockingbird vocalisations. We found a change in the songs' complexity over a period of 57 years, which might be correlated with the loss of genetic diversity in one of the populations. Our study highlights the potential importance of considering behavioural factors, not just genetic factors when planning the reintroduction of endangered species.

4.3 INTRODUCTION

Avian vocalisations are one of the most well-studied examples of complex cultural traits in non-human animals. Three groups of birds, hummingbirds, parrots and oscine songbirds, are known to culturally transmit calls and songs (Jarvis *et al.*, 2000). Although, recently it is been reported some evidence of vocal learning in hand-reared musk ducks (Ten Cate & Fullagar, 2021). The main functions of complex learned vocalizations are related to mate attraction and territory defence, as per the “dual-purpose” hypothesis (Catchpole & Slater, 2003). The influence of learned vocalisations as a signal of reproductive quality has been studied in detail across many songbird species over the last century (i.e., de Kort, Eldermire, Cramer, & Vehrencamp, 2009; Slabbekoorn & Smith, 2002).

Although there is no fixed definition of complexity, commonly used measures of song complexity include repertoire size (diversity), delivery, switching, variation, duration, bandwidth, and inflections per second (Benedict & Najar, 2019). For the sake of simplicity in this paper, we define complexity as a change in the syllable repertoire, song structure and delivery of song which encompass all the measurements mentioned above. Overall complexity of bird vocalisations may be influenced by multiple ecological factors. Song complexity may vary with the age of the bird, where vocalisations of the juveniles are simpler than those of the adults due to learning (Kipper & Kiefer, 2010; O'Loghlen & Rothstein, 1995). Sociality can also influence song complexity, where highly social and cooperative-breeding birds show variation in vocalisations related to social status (Voigt, Leitner, & Gahr, 2007). Additionally, complexity of vocalisations has been related to the complexity of the habitat (Hill, Pawley, & Ji, 2017), breeding stage (Demko & Mennill, 2019), and differences in brain size between sexes (Garamszegi, Eens, Erritzøe, & Møller, 2005).

Geographical variation in songs has been observed in many songbird populations at various spatial scales (Bell, Slabbekoorn, & Jesse, 2003; Galeotti, Appleby, & Redpath, 1996; Kroodsma, 1985; Leader, Yom-Tov, & Wright, 2000). This variation usually arises from a combination of the dynamic song-learning process, and isolation by natural barriers (Podos & Warren, 2007)**.** Over time, cultural evolution (Darwinian theory of cultural change (Mesoudi, 2017) that includes mutations, modifications, innovations, and drift of cultural traits) can lead to innovative behaviours, such as new types of song (Garland *et al*., 2011), and the emergence of local dialects (Aplin, 2016; Laland & Janik, 2006; Parker, Anderson, Jenkins, & Brunton, 2012; Parker, Hauber, & Brunton, 2010; Slater, 2003). Bird vocalizations may change over time in an isolated island population in a similar way to genetic evolution, though potentially more rapidly because new songs being transmitted and learned within and among extant generations (Laiolo & Jovani, 2007; Whitehead, Rendell, Osborne, & Würsig, 2004). In the same way that evolutionary changes of species are influenced by demography, demographic factors are thought to play an important role in the evolution of song. For instance, larger, more productive populations often have greater song repertoires whereas populations prone to extinction tend to have smaller repertoires (Baker, Baker, & Baker, 2001; Laiolo & Tella, 2007; Laiolo, Vögeli, Serrano, & Tella, 2008). Though it is not clear which is the cause or the effect, the correlation between population size and song diversity mirrors that of small populations and inbreeding depression (O’Grady *et al*., 2006; Spielman, Brook, & Frankham, 2004).

Cultural evolution may not be the only process driving the divergence of isolated populations over time. Morphological variation among populations may also drive the development of new dialects. Traits such as the morphology of beaks and vocal tracts (Derryberry *et al*., 2012; Derryberry *et al*., 2018; Huber & Podos, 2006; Podos & Nowicki, 2004; Snowberg & Benkman, 2007), and body size, may affect vocalisations via mechanical constraints on song production (García & Tubaro, 2018; Podos, 1997). Nevertheless, in some endangered species, new local representing culture can develop as a consequence of conservation practices, especially in captive populations (Crates *et al.*, 2021; Martínez & Logue, 2020). In some cases, divergence in vocalizations can lead to cultural reproductive barriers between populations and, eventually, speciation (Irwin, Bensch, & Price, 2001; Slabbekoorn & Smith, 2002).

Over the last decade, cultural evolution has received attention in small or endangered populations. When reproductive success is restricted by culturally transmitted behaviours, identifying scenarios that support the retention of cultural diversity, may become an integral component of a conservation plan (Ryan, 2006). Small populations are often exposed to the negative effects of inbreeding depression. To mitigate this problem, translocating individuals from different populations can improve genetic diversity (Tracy, Wallis, Efford, & Jamieson, 2011). Yet, cultural and behavioural factors may hamper attempts to introduce genetic diversity to populations via translocations. For example, assortative mating based on local dialect preferences could compromise the reproductive success of mixed founder populations and the success of the translocation itself (Bradley, Molles, & Waas, 2014; Parker *et al.*, 2012). For human-assisted conservation efforts such as translocations, regional dialects can lead to assortative mating, where females prefer to mate with ‘familiar’ males due to a strong preference for familiar song types (Martins, Rodrigues, & de Araújo, 2018; Rowe & Bell, 2007). Thus, differential responses to signals from different conspecific populations are considered evidence of a degree of reproductive isolation (Irwin *et al.*, 2001), decreasing the chances of a successful translocation by inhibiting genetic and cultural mixing when multiple sources populations are transferred.

Here, we studied the vocalisations and morphology of the Floreana mockingbird (*Mimus trifasciatus),* an endangered songbird living in two remnant populations that have been isolated since the extinction of the main population on Floreana Island (Grant, Curry, & Grant, 2000). Currently, the Floreana mockingbird is being considered for reintroduction to Floreana Island after the eradication of invasive predators that caused their extinction (Ortiz-Catedral, 2018). Although the genetic consequences of isolation and divergence are well known for the species (Hoeck, Keller, Beaumont, *et al.*, 2010; Hoeck, Keller, Bollmer, & Parker, 2010), the ecological consequences related to the possible cultural evolution and inter-population recognition are unknown. Cultural evolution is especially important for one of the mockingbird population's which shows low levels of genetic diversity (Hoeck, Keller, Beaumont, *et al.*, 2010), as there are known effects of decreasing genetic diversity on the loss of song complexity (Baker, 1975; Paxton *et al.*, 2019).

The overall aim of our study was: 1) To compare vocalisations from the two remnant populations to examine whether mockingbird's songs have changed between the two populations (cultural divergence) when controlling for factors such as sex and age of the individuals. 2) To identify the possible causes that may explain cultural divergence between populations we tested two hypotheses: a) There are morphological differences between populations, and these differences may affect the complexity of vocalizations and create cultural divergence between populations. b) Cultural evolution by drift has had an effect on the complexity of vocalizations of the small population of Champion. We tested hypothesis B only on Champion because of the availability of historical recordings for this population and because the population have experienced genetic drift since the extinction of the main population on Floreana (Hoeck, Keller, Beaumont, *et al.*, 2010).

4.4 MATERIALS AND METHODS

4.4.1 Study site

This study took place on the islets of Champion (90° 23’100’’W 01° 14’240’’S) and Gardner-by-Floreana (90°17’700’’W 01°19’969’’S) in the northern and eastern part of Floreana Island (Fig. 4.1) in the Galápagos Archipelago, Ecuador. Champion is a circular islet of approximately 400 m in diameter and 9.4 ha in size; it is a emerged crater with a maximum elevation of 46 m above sea level and is located 800 m away from the coastline of Floreana Island (Grant *et al.*, 2000). Due to the small size of the islet, the study area covers the entire islet. Gardner-by-Floreana (hereafter Gardner) is an islet of 76.5 ha, located 8 km away from the coast of Floreana; it is a large volcanic cone that has partially sunk creating an islet bounded by cliffs of 50 to 100 m, and reaching an elevation of 210 m above sea level. Our study took place on the only accessible area of this islet, the 100 m high plateau of approximately 12 ha, located in the eastern part of the islet (Jiménez-Uzcátegui, Llerena, Milstead, Lomas, & Wiedenfeld, 2011).

4.4.2 Recordings of wild Floreana mockingbirds

In 2019, we opportunistically recorded vocalisations of individual birds during a period of six days for Gardner and two days for Champion from 0600 to 1200 h and from 1400 to 1800 h (times of the day when the birds are most actively singing). All recordings were made using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) and a portable solid-state recorder (Marantz Professional PMD 661, Marantz Professional, Cumberland, U.S.A.) with 24-bit sampling precision and 48 kHz sampling rate. *Mimus trifasciatus* live in group territories of six or more individuals (personal observation). Dominant males and females sing regularly from specific high perches along with submissive individuals on lower perches. Individuals usually stay within the family group territory but some birds are more mobile (especially juveniles) (Pers. obs.). Recordings were initiated when a bird was located and ended when the bird stopped singing or vacated the perch. Recordings were made on calm days, and the unidirectional microphone was positioned to minimise wind noise. The naïve behaviour of the Floreana mockingbird meant that all recordings could be made within 5 m from the focal bird. Prior to recording sessions, birds were banded by EMRR and LOC as a part of a long-term conservation study under the permit number PC-42-20 from the Galápagos National Park and the Ecuadorian Ministry of Environment. For each recording, we documented the GPS location, date, time of the day, unique colour band combination (when possible) and behaviour. Individuals were generally recorded more than once during each day. Individuals were identified using a Nikon D90 digital camera with 70-300 mm lens and Eagle Optics Ranger 10x42 binoculars. The total number of birds sampled in this study comprised 30% of the global population of the Floreana mockingbird. For the analysis, we only used recordings of birds that could be identified by their bands (7 individuals with 2559 syllables from Champion and 14 individuals with 3856 syllables from Gardner).

4.4.3 Vocalisation categories

Songs of mockingbirds (family Mimidae) are complex and consist of sequences of multiple syllable types (Gammon, 2014) that can be combined in multiple ways to produce a variety of song types (Botero *et al*., 2009). The only descriptions of the behavioural context of vocalisations for mockingbirds in Galápagos are from Vitousek *et al*. (2007), who classified the vocalisations of the Galápagos mockingbird (*Mimus parvulus)* into *"songs"* and *"alarm calls",* and Fusani *et al*. (1994), who classified the vocalisations as *"begging calls", "scold calls", "territorial calls"* and *"alarm calls"*. In this study, we classified the Floreana mockingbird vocalisations into three main categories (Fig. 4.2) matching the terminology used for the vocal array of the northern mockingbird (*Mimus polyglottos)* (Derrickson & Breitwisch, 1992): (1) the submissive call or *"begging"* is a short repetitive syllable given by juveniles and submissive birds in the proximity of an adult or a bird higher in the family hierarchy; (2) alarm or *"hew calls",* which comprise two types of calls, one in response to snakes consisting of a short rasp call, sometimes repetitive, and the other high amplitude short call for threats including owls and observers; and (3) a third category which we called *"chats",* which consist of single calls or *"single chats"*, and continuous chats that here we define as *"chatbursts".* The behavioural contexts of the different types of *chats* were not studied in detail because of time and resource constraints. For the purpose of this research, we eliminated from our dataset the *begging* and *hew calls* due to insufficient numbers of recordings for island comparisons as many of the recordings were from unidentified birds. In this paper, we only focus on the *chats* (single *chats* and *chatburst* combined) because its song potential as a conspecific recognition signal directed to individuals outside the family groups (Botero & Vehrencamp, 2007; Logan, 1985; Logan, Budman, & Fulk, 1983).

4.4.4 Acoustic analysis

We visualized the recordings as spectrograms using the open software *KOE* (Fukuzawa *et al*., 2020), with an FFT window of 512. We retained for analysis only high-quality recordings (i.e. high signal-to-noise ratio – songs with minimal background noise and that did not overlap with other birds' songs). Recordings were segmented into units or syllables, defined as a single note repeated in a specific temporal unit and frequency (Wildenthal, 1965). In *KOE*, for each recording, we extracted the following seven acoustic variables using the *"extract features"* option: (i) duration, (ii) spectral bandwidth mean, (iii) frequency modulation mean, (iv) amplitude modulation mean, (v) goodness of pitch mean, (vi) entropy mean and (vii) harmonic ratio mean. We chose these variables because they are the most commonly used in the bioacoustics literature and because some of them are used as a measure of complexity (Benedict & Najar, 2019; Kershenbaum, 2014). Using ordination by *t*-distributed stochastic neighbour embedding (t-SNE; using a perplexity of 30 and 5000 iterations) and similarity indices, we categorised syllables based on identifiable clusters of syllable types (see Fukuzawa (2020) for details).

For each of the seven acoustic variables extracted from *KOE*, we averaged the values across calls within an individual, giving a single mean value for each acoustic variable for each individual. Each variable was then standardised to have a mean of zero and a standard deviation of one (using the 'normalisation' routine in *PRIMER v7*;(Clarke & Gorley, 2015). We then calculated a matrix of between-individual Euclidean distances using all seven standardised variables. We checked for homogeneity of multivariate dispersions (distance of observations to their centroids) using PERMDISP with 9999 permutations for each variable (Anderson, 2006). Then we used Canonical Analysis of Principal coordinates (CAP, 9999 permutations) (Anderson & Willis, 2003) to determine whether individuals could be correctly assigned to the two populations based on the acoustic variables. We used a one-factor non-parametric multivariate analysis of variance (PERMANOVA) with 9999 permutations (Anderson, 2001) using the Euclidean distance to test for differences in centroids of the two populations. This analysis was repeated to examine the data by origin, age and sex because social status is a factor to be considered when analysing cooperative breeding birds. The transition from subordinates/helpers to dominants/breeders induces the development of new song types (Voigt *et al*., 2007) and there is evidence that song variation is related to the social status in cooperative breeding mockingbirds (Botero *et al.*, 2009; Derrickson, 1987). Here, we did not control for social status, but we controlled for age and sex, factors that play an important role in the social status in the Galápagos mockingbird (*M. parvulus*), a related species of Floreana mockingbird (Curry, 1988a, 1988b). PERMDISP, CAP and PERMANOVA analyses were conducted in *PRIMER-e v7* and PERMANOVA+ software. Then we examined the data graphically using unconstrained non-metric multidimensional (nMDS).

4.4.5 Morphology and vocalisation analysis

We use morphological measurements of individuals captured since 2010 (92 individuals from Champion and 315 from Gardner) as a part of a long-term project monitoring the population dynamics of the species. Individuals were captured, banded and morphological body measurements were taken during the banding process: (1) mass, to the nearest 0.5 g with a Pesola spring balance; (2) bill depth, in vertical plane in the middle of the nares; (3) bill width, in the upper mandible in a horizontal plane in the anterior edge of the nares; (4) tarsus, from the intertarsal joint to the foot joint; (5) wing chord, with the wing in a natural arc and at 90° angle with the radius/ulna; (6) head, from the upper bill tip to the nape and (7) tail length. All measurements were taken to the nearest 0.1 mm. For birds with more than one set of measurements, due to recaptures, we calculated the average of measurements. Age was estimated based on the date of banding until 2020 and sex was assigned using the method described in Chapter 2 where birds with wing chord lengths ≥ 119.5 cm were considered males. Morphological data were assessed for normality and plotted outliers considered to be errors were removed from the dataset.

Using standardised morphological data, we calculated a matrix of Euclidean distances and checked for homogeneity of multivariate dispersion using PERMDISP with 9999 permutations for each factor (population, age and sex). We then used PERMANOVA (9999 permutations) to test for differences in centroids by population, age, sex, and their interactions. We also examined the data graphically using nMDS. All statistical analyses were conducted using *PRIMER-e v7* and PERMANOVA+. To test for the influence of morphology in the vocal divergence, we used the morphological and acoustic data of the 21 individuals used in the acoustic analysis. The vocalisation dataset with the seven acoustic variables was reduced to two axes using a Principal Component Analysis (PCA). PCA was run using the package *Factoextra* and *FactoMineR* in R (Kassambara & Mundt, 2019; Lê, Josse, & Husson, 2008; Team, 2013). Finally, the two PCs axes were regressed against beak-related morphological traits (head-bill, depth and width), weight, sex, age and populations as fixed effects using a multivariate linear model in the R package *RRPP* that allows the use of multivariate response data (Collyer & Adams, 2018). Model selection was based on the lowest AIC.

4.4.6 Historical recordings analysis

We obtained four digitalized recordings of vocalisations of the Floreana mockingbird in January 1962 from the Macaulay Library (Cornell Lab of Ornithology). Recordings were made by a single person (Robert L. Bowman) on Champion Islet using a NAGRA III tape recorder connected to an American D-33 microphone in a 76.2 cm aluminium parabola set on the mono channel. We assume that each recording was made of a different individual bird. We discarded one recording due to it being *hew calls.* From the remaining three *chatburst* recordings, we extracted 1224 syllables using *KOE.* For the comparison with the current vocalizations, we only used a subset of *chatburst* recordings from

Champion. We were aware of potential differences added by possible tape degradation of historical recordings over time. Nevertheless, recordings made by the same person at the same time showed high sound quality (Goodale & Podos, 2010). Hence we did not conduct any test to assess tape degradation described in Derryberry (2007) because of our small sample size. Then, we used KOE to extract the same set of acoustic variables described above. We created a data matrix combining the values of the acoustic variables from the historical recordings and the acoustic values of Champion *chatburts*. We ran the same statistical analysis described for interpopulation vocalisations for this new data set (PERMDISP, CAP and PERMANOVA).

4.5 RESULTS

4.5.1 Interpopulation Vocalisations

We found no significant difference in multivariate dispersion of the acoustic variables between populations (PERMDISP, F = 0.42, P = 0.60; Champion mean dispersion = 1.95 ± 0.51, n = 7; Gardner mean dispersion = 2.29 ± 0.28, n = 14) or by sex (PERMDISP, F = 0.01, P= 0.92; female mean dispersion = 2.29 ± 0.39, n = 8; male mean dispersion = 2.24 ± 0.31, n = 13), or between ages (PERMDISP, F = 1.60, P = 0.87).

The CAP analysis produced a single axis to discriminate between the two populations ($\delta_1^2 = 0.81$). The CAP allocated 76% of individuals to the correct population based on the acoustic data, using a leave-one-out cross-validation procedure. PERMANOVA analysis found a significant difference in centroids between populations (pseudo-$F_{1,19} = 2.20$, $P = 0.04$). No significant differences in the vocalizations were found for age (pseudo-$F_{5,15} = 1.66$, $P = 0.12$) or sex (pseudo-$F_{1,19} = 1.30$, $P = 0.25$). The nMDS plot showed some separation between the populations (Fig. 4.3 a).

4.5.2 Morphology and vocalisations

There was no significant difference in multivariate dispersion of the morphological variables between populations (PERMDISP, F = 2.15, P = 0.14; Champion mean dispersion = 6.66 ± 0.28, n = 92; Gardner mean dispersion = 7.22 ± 0.19, n = 315) or by sex (PERMDISP, F = 0.13, P = 0.72; female mean dispersion = 5.71 ± 0.18, n = 236; male mean dispersion = 5.81 ± 0.22, n = 171). There was a highly significant difference in multivariate dispersion between ages (PERMDISP, F = 2.94, P = 0.001).

There was a significant difference in multivariate body measurements by location (PERMANOVA pseudo-$F_{1,405}$ = 16.71, P = 0.0001), age (PERMANOVA pseudo-$F_{11,395}$ = 4.02, P = 0.001) and by sex (PERMANOVA pseudo-$F_{1,405}$ = 213.19, P = 0.001). We did not find any significant interaction between population and sex (PERMANOVA pseudo-$F_{1,371}$ = 0.42, P = 0.66), or between the three factors (PERMANOVA pseudo-$F_{5,371}$ = 0.63, P = 0.79), but we found a significant interaction between population and age (PERMANOVA pseudo-$F_{8,371}$ = 1.68, P = 0.05). In addition, the nMDS plot showed some difference between the populations (Fig. 4.3 b). From the 27 models of the multivariate linear regression that were compared (Table 4.1), the model of the two PCs axes as a function of width, sex, age and population presented the lower AIC, was statistically significant ($F_{4,16}$ = 3.35, p <0.01) and explained the 45.6% of the total variation of the two responses variables. In this model we found that width (β_1= 1.86, p< 0.01) and population (β_4= 2.08, p<0.01) significantly predicted the acoustic variation of the two PCs axes.

4.5.3 Historical vs current vocalisations

Vocalisations from 1962 were not significantly more variable than current recordings vocalisations (PERMDISP, F = 2.93, P = 0.30; historical mean dispersion = 1.74 ± 0.40, n = 3; current mean dispersion = 1.05 ± 0.19, n = 4). A single canonical axis was calculated for the CAP analysis ($\delta_1^2 = 0.89$). The leave-one-out cross-validation allocation of observations assigned an individual to a time period with a 100% (7/7) accuracy. PERMANOVA results showed a significant difference between the centroids from historic and current recordings (pseudo-$F_{1,5} = 9.06$, $P = 0.03$).

4.6 DISCUSSION

We found significant differences in the acoustic characteristics of songs from two populations of the Floreana mockingbird and shown that individuals could be assigned to a specific population with high accuracy. These differences are consistent with our hypothesis that cultural divergence has occurred since the populations became isolated. This divergence is likely to be due to cultural evolution by a combination of processes including cultural drift (random deletion of song types), cultural innovation (mutations that result in new song types) (Marler, 1970; Mundinger, 1980), and biomechanical effects produced by morphological variations between the populations (Podos & Nowicki, 2004). Concurrent with the vocal differences, we also detected a difference in the morphology between the two populations and the influence of beak width in the variation of the vocalizations. Furthermore, we found differences in acoustic variables in the mockingbird’s vocalisations over a period of 57 years in one of the populations, which could be interpreted as a sign of cultural drift.

Cultural divergence usually arises as a consequence of social learning to maximize the fitness among individuals of the same population, or as a result of inter- and intrasexual selection (Baker, 1975) and these changes in culture can happen in short time frames and entire regions (Otter, Mckenna, LaZerte, & Ramsay, 2020). Several factors related to isolation and local adaptation may have contributed to the cultural divergence between the two populations. In cooperative breeding birds, there is a correlation between song complexity and social group size (Freeberg, 2006; Freeberg, Dunbar, & Ord, 2012). Different species of Galápagos mockingbirds show a different level of group structure and social organization, even between populations of the same species (Curry, 1989). However, the differences in the group structure among populations of the Floreana mockingbirds have not been studied yet. Further, some studies show the influence of the habitat on song complexity in vocally complex songbirds. For instance, in the tūī (*Prosthemadera novaeseelandieae*), an endemic honeyeater from New Zealand, and for the skylark (*Alauda arvensis*), habitat structure influences song sharing and song complexity (Briefer, Osiejuk, Rybak, & Aubin, 2010; Hill *et al.*, 2017). Tūī living in habitats with a complex plant community show higher values of spectral complexity (entropy) and longer song duration. In the skylark, habitat seems to influence the composition and sharing of syllables but not their complexity. Although Champion and Gardner have similar vegetation types, there is differentiation in phenotypic features (Champion is arboreal and Gardner is shrubby) and density of *Opuntia* cactus (*Opuntia megasperma*) on both islets (Curry, 1986) (Ascencio *et al.*, in preparation) that might influence the habitat structure and thus the song transmission in the respective acoustic environment (Derryberry *et al.*, 2018).

Geographic isolation and differences in habitat structure can lead to differentiation in morphological traits, especially in multipurpose structures such as birds' beaks. Such differentiation can be more pronounced between populations when they vary in specialized trophic niches and climates (Friedman *et al*., 2019; Grant & Grant, 1989, 1993; Slatkin, 1985). The differences in morphology we found between populations were large. In particular, the width of the beak was associated with the acoustic variability between populations. However, despite the significant difference in all the morphological traits between populations, sex, and age, only the interaction age-sex seemed to have a significant influence on the vocalisations. Other studies have shown similar correlations between beak morphology and song variation. For example, Demery *et al*. (2021) found in a phylogenetical level analysis of the tanagers (Thraupidae) that bill size and shape influence distinct elements of song, independently of the covariation of body size, with beak size influencing temporal variables, and beak shape influencing trill rate. Similarly, Derryberry *et al*. (2018) in their study with ovenbirds (Furnaridae), showed that both body mass and bill size influence frequency and temporal aspects of the song. Moreover, Garcia & Tubaro (2018) found a similar pattern studying the "blue cardinalids" (Cardinalidae) where the shape of the bill was correlated with song variation. In contrast, Slabbekoorn and Smith (2000) did not find this correlation between bill size and song in the African finch (*Pyrenestes ostrinus*) a species with a high degree of beak polymorphism. In our study, we highlight the importance of beak morphology on the song variation of the Floreana mockingbird. Yet, we cannot specify if the correlation is explained by the size or shape of the width, because we only took one standard width measurement. Morphological variation in beak traits is expected as a result of either drift, selective pressure (biotic and abiotic), local adaptation or geographic isolation (lack of gene flow) and has been demonstrated in other Galápagos birds (Bollmer *et al*., 2003;

Santiago-Alarcon, Tanksley, & Parker, 2006). More studies are needed to clarify the relation between morphology, local adaptation, and song in this species.

Three alternative scenarios could explain the cultural divergence in the Floreana mockingbird. Firstly, it may be due to a founder effect. When Gardner islet separated from Floreana Island due to the sea rise of the inter-glacial cycle (Geist, 1996), only a portion of the acoustic diversity from Floreana may have been retained on Gardner. In contrast, the population on Champion remained connected to Floreana Island because its closer proximity (less than 1km of separation between islands), facilitating the continual exchange of cultural traits through migration of individuals between the islands. Secondly, when the Floreana population became extinct around 1880 (Curry, 1986), the Champion population became isolated. Because isolated populations have a lower rate of syllable change because of the lack of immigration, the consequences of founder effects are more evident (Baker *et al*., 2001). Finally, unlike Gardner, Champion is a small islet (9.4 ha) with a small population. This could induce a strong effect of cultural drift (as happened with genetic drift), accelerating the cultural divergence by loss of complexity. This scenario might be parallel to the genetic drift reported for the population (Hoeck, Keller, Beaumont, *et al*., 2010; Hoeck, Keller, Bollmer, *et al*., 2010). Our results show that current vocalisations are clearly different from the vocalisations of 1962, suggesting a loss of song complexity in this population over the last 57 years. We must acknowledge that the strength of our conclusions is limited by our small sample size; unfortunately, historical recordings are scarce. Nevertheless, loss of cultural complexity over time has been demonstrated in other small populations of endangered insular birds (Paxton *et al*., 2019; Tanimoto *et al*., 2017).

4.6.1 Implications for conservation reintroductions

Floreana mockingbirds are proposed for reintroduction to Floreana Island (Ortiz-Catedral, 2018) as a part of the Floreana Island Restoration Project. To date, only genetic factors have been considered when planning the reintroduction of this species. As a result, the proposed Floreana Island population would source birds from both existing populations to maximise genetic diversity (Bozzuto, Hoeck, Bagheri, & Keller, 2017; Hoeck, Keller, Beaumont, *et al.*, 2010). No other behavioural or ecological aspects of the species have been considered until now, nor any negative consequences of moving birds with different vocalisations. To the best of our knowledge, the only modern case of interaction between mockingbirds with different vocalisations has been between the Floreana mockingbird and San Cristobal mockingbird (*Mimus melanotis)* and seem to result in an interspecific aggressive behaviour (Ortiz-Catedral, Lichtblau, Anderson, Sevilla, & Rueda, 2021). Nevertheless, there is evidence of temporary co-occurrence of two species of mockingbirds (*M, parvulus* and *M. melanotis*) on a single island, showing that Galápagos mockingbirds could hybridize (Nietlisbach *et al.* ,2013).

With our study, we highlight cultural differences that may hinder gene flow and the success of the reintroduction. It is well known that assortative mating can arise as a problem in translocated populations. For example, the North Island Kokako (*Callaeas wilsoni*), an endemic duetting songbird of New Zealand, has been the focus of intensive translocations from multiple source populations, with a high rate of assortative mating between birds from the same source populations having been observed (Bradley *et al.*, 2014). Nevertheless, cultural divergence is not always an impediment to gene flow between populations. Research on both closed- (only juveniles learn new songs) and open-ended (birds learn new songs throughout their life) song learners have been found that specific dialects are not correlated with a specific genetic structure (Leader, Geffen, Mokady, & Yom-Tov, 2008; Ortiz-Ramírez, Andersen, Zaldívar-Riverón, Ornelas, & Navarro-Sigüenza, 2016). In closed-ended learners, dispersing birds are exposed to different dialects and may not express preferences for a specific dialect for mating (Poesel *et al.*, 2017), or only retain the dialect that matches the area where they choose to breed (Nelson, 2000). For open-ended learners, dispersing birds may learn their vocalisations after dispersal, to ensure territory establishment and benefits from sociality (González & Ornelas, 2014).

Mockingbirds are considered open-ended song learners (Gammon, 2020) and are known for their ability to mimic vocalisations, even those of other species (i.e., “heterospecific” songs) (Botero & Vehrencamp, 2007; Gammon, 2014; Howard, 1974). In some cases, mimicry, and incorporation of songs from other species could also contribute to the divergence of songs between populations. For example, the incorporation of heterospecific songs in Regent honeyeater (*Anthochaera phrygia*), another endangered species from Australia, has contributed to the divergence of songs and also a low reproductive success (Crates, 2019; Crates *et al.*, 2021). Further, in the case of the Dupont’s Lark (*Chersophilus duponti*), a species that does not imitate other birds, song diversity increases in small populations (Laiolo *et al*., 2008). In the case of the Floreana mockingbird, mimicry and open-ended learning have not been reported or studied yet. Nevertheless, mimicry seems an unlikely cause of vocal divergence, because of both islets share the same diversity of bird’s species. However, the possibility that the Floreana mockingbirds are open-ended song learners might facilitate the recognition and/or incorporation of foreign dialects between the two populations. Before any attempts to reintroduce the Floreana mockingbird, more studies regarding signal responses using playback experiments are needed to assess the possible impact of assortative mating and/or recognition of local dialects between populations. From a conservation viewpoint, it is necessary to anticipate cultural barriers to maximise the genetic diversity of a multi-sourced reintroduction to Floreana Island prior to implementation.

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Data accessibility

The datasets used in preparing this paper are available from the corresponding author on reasonable request. Recordings used in this study have been archived at The Macaulay Library at the Cornell Lab of Ornithology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

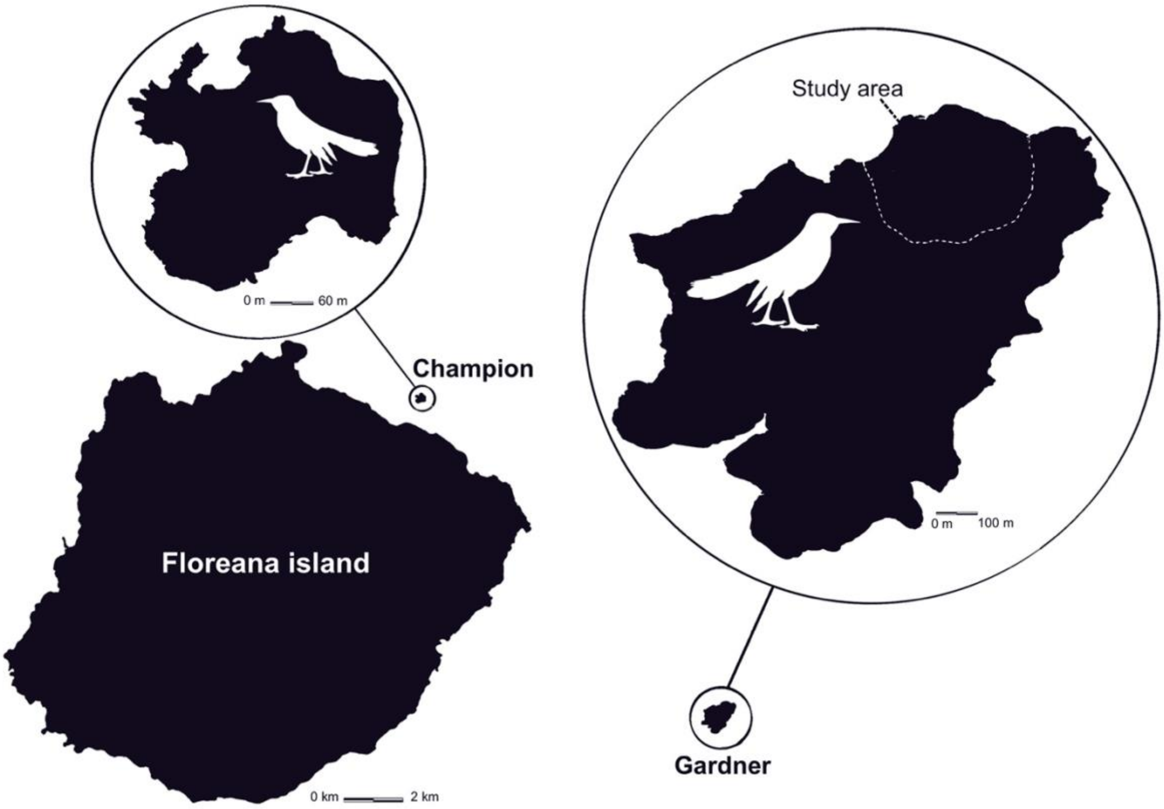


Figure 4.1 Close up of Floreana Island with the study islets, Champion in the northeast and Gardner in the southwest. Art. Simone Giovanardi.

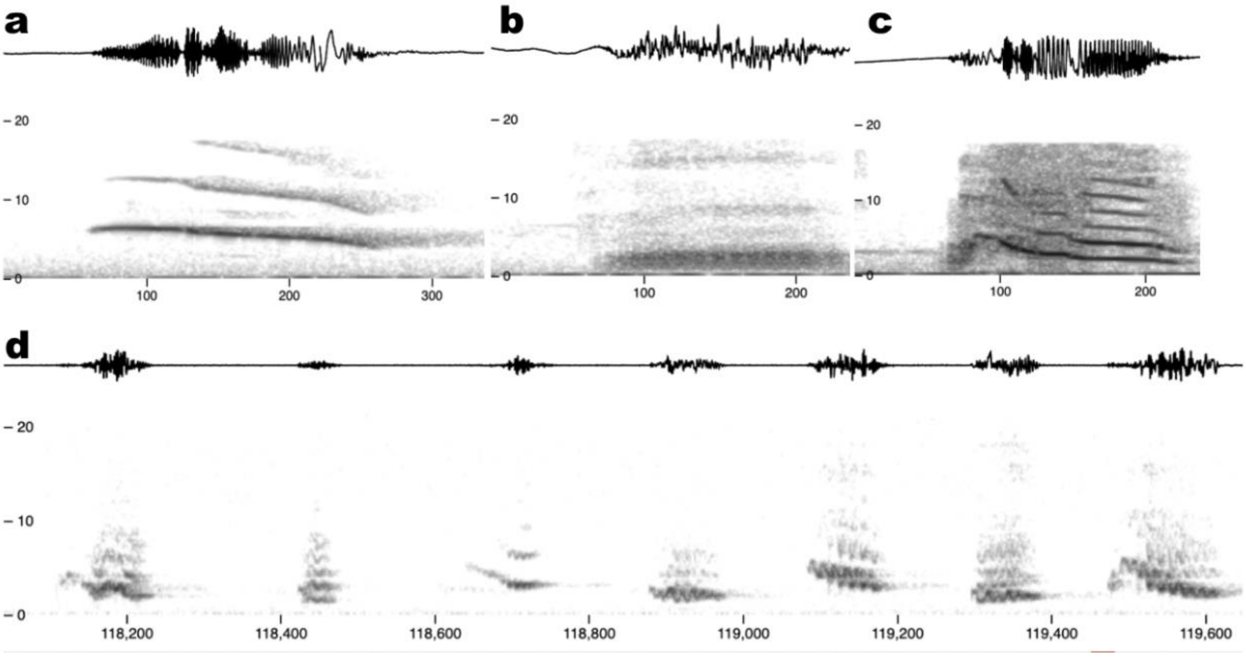


Figure 4.2 Spectrograms of the different types of Mimus trifasciatus vocalisations recorded during this study, a) begging call, b) hew call for snakes, c) hew call for other threats and d) example of the diversity of chats used for the analysis in this study.

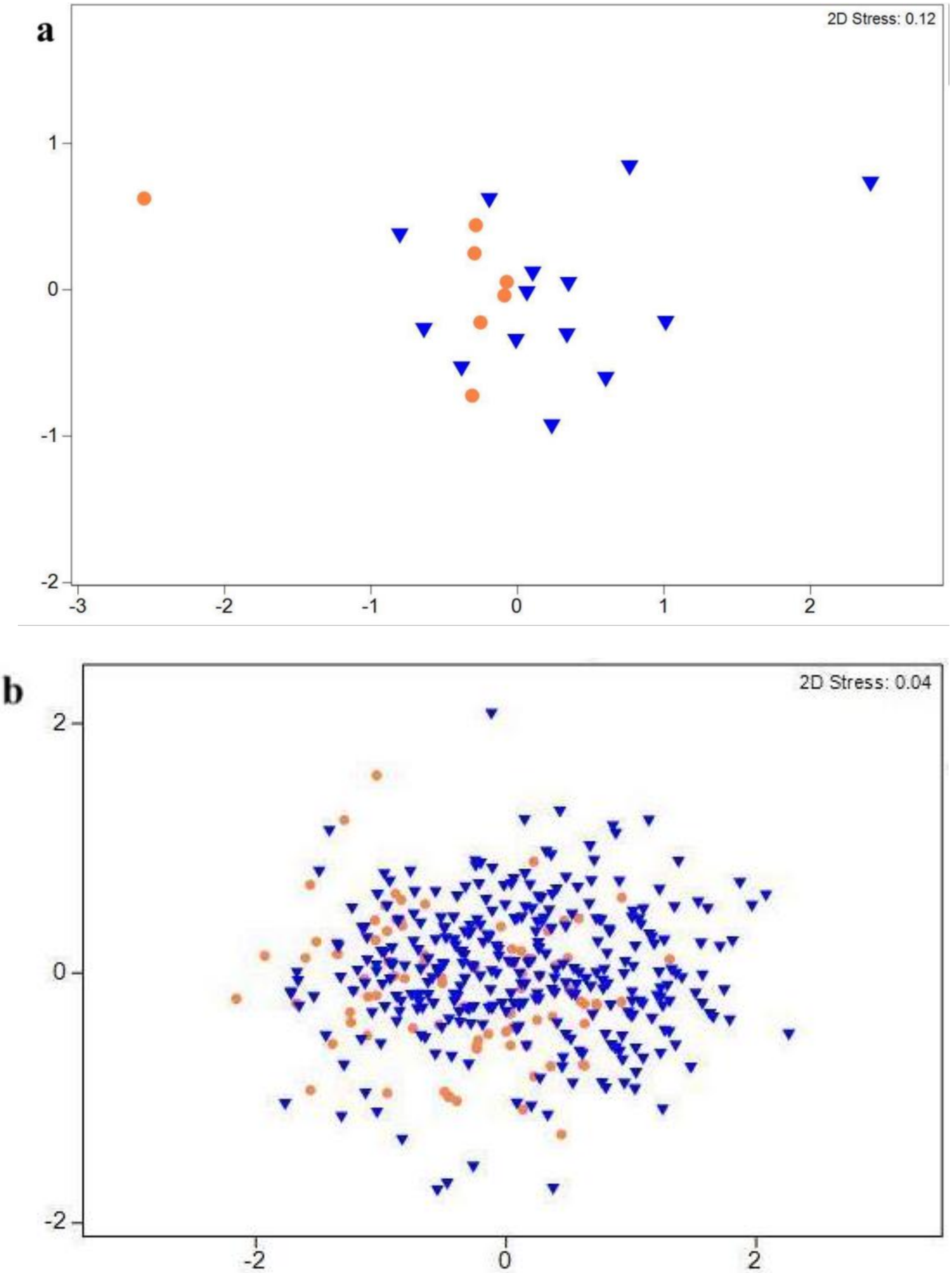


Figure 4.3 Unconstrained nMDS ordination of **a)** seven acoustic variables and **b)** morphological measurements of Floreana mockingbirds. Orange circles = Champion, , blue triangles = Gardner. Scale in the nMDS are arbitrary. Stress values indicate a good representation of the reduced dimensions.

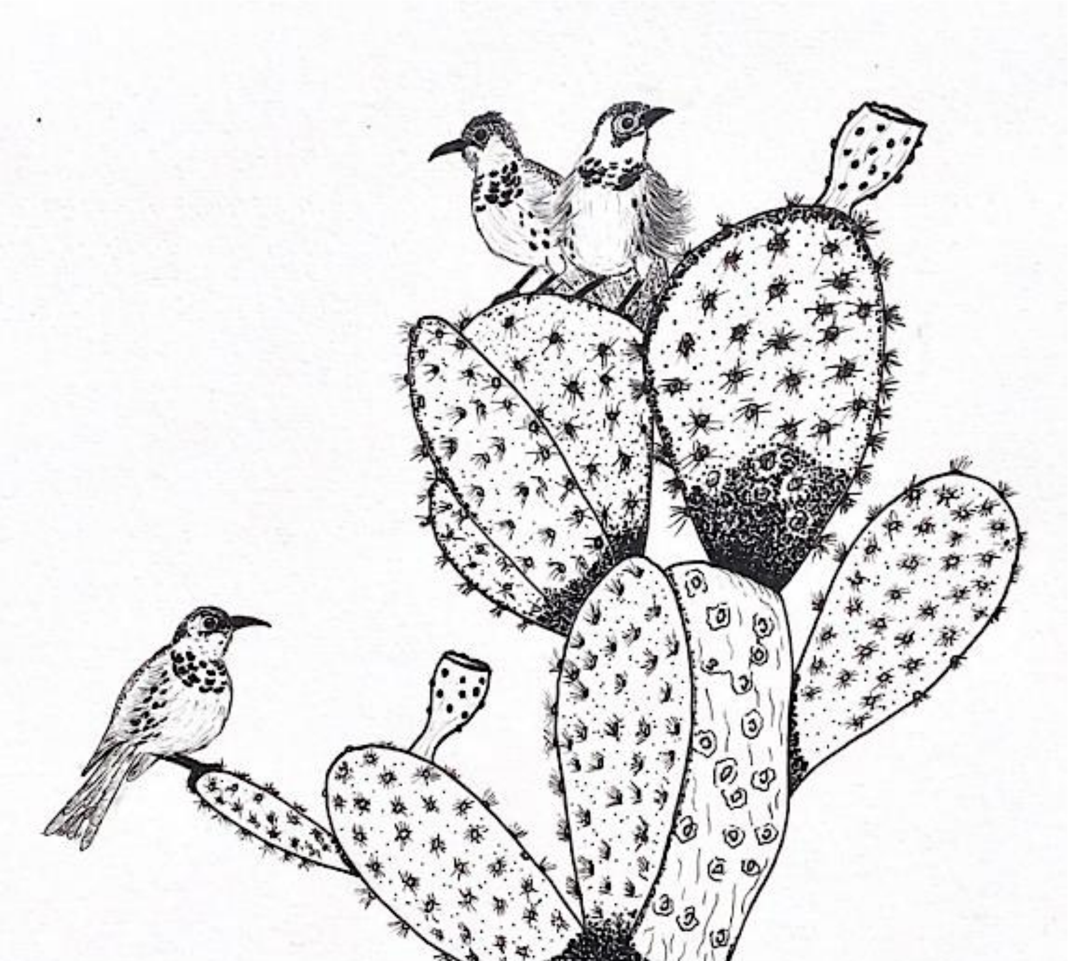
Table 4.1 Summary of the multivariate linear models built in the *RRPP* package. Models are ranked from the lowest Akaike Information Criterion (AIC) and model penalty.

Models	**AIC**	**Penalty**
Width + Age + Sex + Population	149.227	26
Width	150.352	14
Age + Sex + Population (null)	150.985	22
Depth + Width + Age + Sex + Population	151.487	30
Width + Age	151.679	18
Width + Population	152.041	18
Width + Sex	152.391	18
Age	152.496	14
Head + Width + Age + Sex + Population	152.887	30
Weight + Width + Age + Sex + Population	153.051	30
Depth + Age + Sex + Population	154.001	26
Head + Age + Sex + Population	154.576	26
Weight + Age + Sex + Population	154.900	26
Weight + Width + Depth + Age + Sex + Population	155.319	34
Weight + Width + Head + Age + Sex + Population	156.134	34
Depth	156.360	14

Depth + Width + Weight + Head + Sex + Population	156.566	34
Population	157.141	14
Head + Depth + Age + Sex + Population	157.589	30
Depth + Width + Weight + Head,	157.823	26
Weight + Depth + Age + Sex + Population	157.890	30
Weight + Head + Age + Sex + Population	158.571	30
Depth + Width + Weight + Head + Age + Sex + Population (full)	158.579	38
Sex	159.024	14
Head	160.799	14
Weight	161.009	14
*Depth + Width + Weight + Head + Age + Sex + Population + Depth*Width*	162.280	42

Chapter 5

Hierarchy, structure and disruption of the dominance network in the endangered cooperative breeding Floreana mockingbird: the importance of social structure in a reintroduction scenario.



Three Floreana mockingbirds perching in an Opuntia cactus.

Mangere Island, February 2022

Enzo M. R. Reyes

5.1 HIERARCHY, STRUCTURE AND DISRUPTION OF THE DOMINANCE NETWORK IN THE ENDANGERED COOPERATIVE BREEDING FLOREANA MOCKINGBIRD: THE IMPORTANCE OF SOCIAL STRUCTURE IN A REINTRODUCTION SCENARIO.

Enzo M. R. Reyes[1*], Smith, A.N.H.[1], Rueda, D.[2], Sevilla, C.[2], Brunton, D. H.[1] & Luis Ortiz-Catedral[1,3]

[1] Ecology and Conservation Lab, School of Natural and Computational Sciences, Massey University, Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand.

[2] Galápagos National Park, Puerto Ayora, Galápagos, Ecuador.

[3] World Parrot Trust, Glanmor House, Hayle Cornwall TR27 4HB, United Kingdom.

*Corresponding author: enzorreyesb@gmail.com

5.2 ABSTRACT

Cooperative breeding is a breeding system present in hundreds of birds around the globe. Despite social structure and dominance having been studied in a few species that display cooperative breeding, the importance of this level of sociality has not been explored in the context of translocations of endangered species. Here we used a social network approach and Exponential Random Graph Models (ERGM) to investigate the hierarchy and social structure of the endangered cooperative breeding Floreana mockingbird, with

the aim of using the network information to build simulations of social disruption in different translocations scenarios. We found that mockingbirds hierarchy is highly transitive and that the main attribute that influence mockingbird dominance network is age-related. Finally, we showed how harvesting individuals with different networks' importance could contribute to the social rupture of the groups. The results presented in this study highlight the importance of avoiding group rupture by studying the social behaviour of highly social species before any management actions are planned to improve the conservation status of endangered species.

5.3 INTRODUCTION

Cooperative breeding (CB) in birds is defined as a breeding system where parental care is provided by parents and helpers, that are typically genetically related (Cockburn, 2006). CB is a complex and rare social system present in more than one hundred bird species, where the main difference with colonial birds is the presence of helpers (Brown, 1978). Helpers are typically related juveniles (Temple, Hoffman, & Amos, 2009) or sexually mature birds in a status of reproductive suppression, due to few breeding opportunities or low rates of reproduction within the family group (Lundy, Parker, & Zahavi, 1998). The role of helpers in CB systems varies from direct food provisioning to chicks, territorial defence and even sharing incubation duties (Craig & Jamieson, 1990; Curry, 1988a, 1988b; Temple, 2006). Although multiple hypotheses, including social and ecological factors, have been proposed to explain the evolution of CB, to date, phylogenetic history is the best predictor of the occurrence of CB in birds (Ligon & Burt, 2004).

Social interactions are one of the most important attributes of population ecology in vertebrates, especially in highly social CB species that exhibit complex social structures and hierarchies. Such behavioural traits can affect population growth rate, increase reproductive skew, and influence effective population size; an important consideration for conservation management planning (Anthony & Blumstein 2000). The viability of a wild population is strongly associated with the social interactions between its members, different processes that fragment social interactions can have long term consequences at both individual and population levels (Banks, Piggott, Stow, & Taylor, 2007). For instance, the loss of individuals (through mortality or dispersal) with different social importance could collapse or disrupt an entire social group (Beisner, Jin, Fushing, & Mccowan, 2015; Flack, Girvan, De Waal, & Krakauer, 2006; Piefke, Bonnell, DeOliveira, Border, & Dijkstra, 2021; Williams & Lusseau, 2006). Similar to mortality or dispersal events, conservation actions like translocations can disrupt social interactions in highly social species, potentially risking the success of the conservation action. To minimize these risks, there is some evidence that moving entire social groups may help to avoid group disintegration and ensure fidelity to the new sites in translocations (Clarke, Boulton, & Clarke, 2002). For example, in translocated groups of black-tailed prairie dogs (*Cynomys ludovicianus*), their social structure was kept intact and were more likely to survive and reproduce than those released without family groups (Shier, 2006).

Social network analysis (SNA) is a recent, and increasingly popular, tool used to investigate associations and interactions between individuals. SNA is a framework that quantifies social structure at multiple levels e.g. individuals, groups or populations (Croft, Madden, Franks, & James, 2011). In SNA, individuals of a monitored population are represented as nodes (or vertex) connected to each other, with associations or interactions between two individuals represented by ties (or edges) (Pinter-Wollman *et al*., 2013). One of the key objectives of SNA is to quantify the position of an individual in the social network structure (Snijders *et al*., 2014). Despite being a powerful tool in behavioural studies, the usefulness of SNA in the field of conservation is not fully developed. Nonetheless, this type of analysis could likely be applied to minimise social group dissolutions caused by translocations, by identifying key individuals that are essential for maintaining social stability (Dey, Reddon, O'Connor, & Balshine, 2013; Snijders, Blumstein, Stanley, & Franks, 2017). Hence the importance of the SNA in the context of translocations, where socially cohesive groups need to be released together to minimize the stress of the relocation process and facilitating rapid establishment in a new area (Lyles & May, 1987).

Network’s centrality and density are well-known basic measures that explain the connectivity properties of social networks. However, these two measurements are not enough to explain some aspects of complex social behaviour, because the patterns of clustering can be explained by several variables of self-organization, structural balance or node-level effects (Robins, Pattison, Kalish, & Lusher, 2007). Exponential random graph models (ERGM) could work as a suitable tool to study the structure of social networks, because it allows the modelling of multiple variables at the same time, accounts for directed interactions (even weighted interactions between nodes), and the evaluation of the model through simulations (Snijders, Pattison, Robins, & Handcock, 2006; van der Pol, 2019; Wasserman & Pattison, 1996). ERGMs are somewhat analogous to logistic regressions (Dey & Quinn, 2014; van der Pol, 2019) and have been used in other studies of SNA, but mainly in the social sciences (Goodreau, Kitts, & Morris, 2009). Furthermore, ERGMs have been used in CB species, where the main objective was to model the interactions of dominance and hierarchies between family groups (Dey & Quinn, 2014; Dey, Tan, O’Connor, Reddon, & Caldwell, 2015), and establish the importance of individuals that maintain social cohesion (Wey & Blumstein, 2010). Moreover, ERGMs allow the modelling of the behaviour that creates the social interaction and the social network structure (Silk & Fisher, 2017); using parameters of node-base covariates as same-sex relationships (homophily), age and body size attributes where ties are modelled in response to the attributes (Silk & Fisher, 2017), spatial proximity and link duration of the individuals (Edelman & McDonald, 2014).

In this paper, we investigate the structure of the hierarchy, social network and the probability of group breakup in the Floreana mockingbird (*Mimus trifasciatus*), a CB bird and the rarest mockingbird of Galápagos Islands. Mockingbirds in the Galápagos display a wide range of social organizations depending on the species and the island where they are present. Four species of mockingbirds are recognized in the archipelago and all of them are allopatric, with three species living on a single large island (*Mimus melanotis* on San Cristobal Island, *M. macdonaldi* on Española, *M. trifasciatus* restricted to Floreana Islets) and one species widespread throughout the archipelago (*M. parvulus*) (Arbogast *et al*., 2006). The social structures range from socially monogamous pairs without helpers, and trios without helpers holding large territories in *M. melanotis,* the least social of all the Galápagos species (Curry, 1989), to extensive family groups in *M. macdonaldi* (Von Lippke, 2008). In addition, social structures range from singular CB where only the dominant pair breed, to plural CB where more than one pair breed within the boundaries of a family group territory in *M. parvulus* and *M. trifasciatus* (Curry, 1988a) and *M. macdonaldi* (Von Lippke, 2008).

Although other Galápagos mockingbirds have well documented social structures, this aspect of the Floreana mockingbird ecology is poorly described. Social structure has been explored in only one of the two populations of the species. These descriptions are limited to the small population on Champion where the population fluctuates between 20 to 50 individuals because the habitat saturation (Grant *et al*., 2000). In Champion, Floreana mockingbirds have been reported as an obligate cooperative breeder, with groups composed of a dominant alpha male, one alpha female and up to four submissive birds or helpers (Curry & Grant, 1989). Therefore, they are categorized as mostly singular breeders but with exceptional cases of plural breeding (Curry, 1989; Curry & Grant, 1990). Limited availability of habitat is one of the principal hypotheses proposed for CB (Brown, 1974; Emlen, 1982) and is believed to be the main mechanism that influences the social organization in all the Galápagos mockingbirds (Curry, 1989).

We use SNA applied to field observations of three family groups to: 1) To identify the dominance hierarchy structure of the Floreana mockingbird in both extant populations. 2) Identify the dominance network structure by exploring group and individual attributes such as: a) size differences between birds, with larger individuals being dominant over smaller individuals; b) differential homophily of social status, where we associate age as a measurement of social status based on the assumption that older birds have higher social status within the family groups (Curry, 1988), with older birds more dominant to younger birds; c) sexual homophily, where dominance is more likely to happen between same sex-dyads; d) the effect of age on giver and receiver dominance, where we expect younger birds are the receiver of dominance; e) reciprocity, where we test for the probability of mutual dominance interactions. 3) Finally, we test the probability of social disruption by the hypothetical removal of important individuals in the social network, simulating different scenarios of harvesting for a reintroduction.

5.4 METHODS

5.4.1 Study area and field methods

This study took place during July/August 2019 on the islets of Champion (90° 23’100’’W 01° 14’240’’S) and Gardner-by-Floreana (90°17’700’’W 01°19’969’’S) located in the northeast and southeast of Floreana Island-Galápagos Archipelago (Fig. 5.1). Further details about the study area can be found in Chapters two, three and four. The study area on Champion was limited to the southeast part of the islet where only one family group was monitored. In the 12-ha area monitored on Gardner-by-Floreana (hereafter Gardner), we focused on two adjacent family group territories. Floreana mockingbirds are highly territorial and live in family groups of different sizes. In this study, we selected social groups in which all the individuals were banded (except by yearling birds that were banded during this study) with aluminium colour rings, to facilitate individual recognition at a distance and the identification of dominance interactions between individuals. During banding, a set of morphological measurements were taken (described in the methods of Chapter 2). It is possible to estimate the age of most birds in this study. Juveniles were identified based on their distinct plumage and adults were aged based on the year of banding, as banding in the study area started in 2006. Finally, sex was determined by wing chord measurements using methods described in Chapter 2.

5.4.2 Dominance observations

Behavioural observations were conducted during the non-breeding season on one family group on Champion Islet and two family groups on Gardner Islet. Observations were conducted from 6:30 to 17:30 h. Focal groups were observed for 60 minutes in the morning and another 60 minutes in the afternoon during a period of four days for Gardner and two days for Champion (time in Champion was reduced because of logistic constraints). Observers walked into the focal family group territories recording any opportunistic interactions between birds. Territories boundaries has been already plotted by Ortiz-Catedral (unpublished) and (Grant, Curry, & Grant, 2000) on Champion Islet. Meanwhile on Gardner, territories were inferred by the GPS position of the birds during the first few days of banding and re-sighting. Interactions between individuals were recorded using a 50-300 mm Nikon lens and Eagle Optics Ranger 10x42 binoculars. Dominance was recorded during two forms of interactions within family groups: aggressiveness (pecks and chasing (Hatch, 1966)) and submission (submissive crouched posture (Hatch, 1966)). Furthermore, senders and receivers of the interactions were recorded. Interactions between members of the focal group and other family groups were not included in this analysis but consisted of members of the observed group chasing away intruder individuals from other groups. Floreana mockingbirds are habituated to the presence of researchers, but to minimize any disturbance of normal activities on the birds, the observer presented themselves 10 minutes prior to the observations for acclimatation. Mockingbirds are curious but usually loss interest in humans quickly.

5.4.3 Statistical analysis

Dominance hierarchy structure. Using the behavioural observations described above, were created a directed binary matrix of dominance interactions (aggressiveness and submission pooled) (Croft, James, & Krause, 2008) for each family group. Birds were represented by nodes and the presence (1) or absence (0) of interactions were indicated by the edges of the network. To create directionality, the edges of each matrix were arranged by senders as rows and receivers as columns. To test our first question, we used the triangle transitivity method of Shizuka & McDonald (2012) that is equivalent to linearity (De Vries, 1995). This method measures the proportion of groups that form transitive triads (t_{tri}) as opposed to cyclical triads (see Holland & Leinhardt 1976). Finally, t_{tri} and its statistical significance were calculated in the *statenet* package in R (Handcock, Hunter, Butts, Goodreau, & Morris, 2008) following the codes of Shizuka and MacDonald (2012) and its corrigendum in 2014. P values were combined using the Fisher method in the *poolr* package in R (R Core Team, 2013).

Dominance network structure. To identify the structure of our network we created a super-matrix containing the three groups. For this analysis, the matrix used was directed and weighted. This means that the exact number of interactions between dyads were recorded and specified as an edge attribute of the network. For the body size attribute, instead of using a single morphological measurement as a proxy of body size, we used the Scaled Mass Index (SMI) of the mass and the head-bill morphometry using the method described by Pieg & Green (2009). We performed a ERGM with the following stats in our model: *sum* (intercept), *non_zero*, *node_factor* for sex, *node_match* (for sex and age), *abs_diff* (for SMI), *node_ocov* and *node_icov* (for age), and *mutual* (for reciprocity). More details regarding the statistic terms of the model can be found in Morris, Handcock and Hunter (2008). Additionally, we tested for the degeneracy of the model using Marcov Chain Monte Carlo (MCMC) diagnosis of the package ERGM, for more details about model degeneracy see Handcock *et al*. (2003). Finally, because goodness of fit methods have not been developed yet for weighted networks, we evaluated the resemblance of the mean of the simulated networks using the statistics of the observed network.

Reintroduction harvesting simulation. Following similar methods applied in social and physical sciences (e.g. Albert, Albert, & Nakarado, 2004; Wood, 2017), we calculated the betweenness-centrality and degree using *statenet* package (Handcock *et al*., 2008) in R (R Core Team, 2013). Betweenness of a node is defined as the number of shortest paths in which a node lies on within the network (Goh, Kahng, & Kim, 2001; Newman, 2001). Meanwhile, degree is the number of edges with which a node is connected (Croft, James, & Krause, 2008). Further, we identified cut-points (brokers) that are nodes that when removed affect the flow and connectivity properties of network (Burt, 1992; Burt, 2000). We simulated a “harvesting for reintroduction” scenario by removing individuals from the network. With the aim of reproducing a network dynamic, our simulation of harvesting consisted of relocating up to 50% of individuals from each family group. We simulated four different scenarios with different node “removals”. 1) Age importance: Oldest birds were taken in a five individuals translocation group. 2) Node importance: Individuals with high betweenness were excluded from harvest (for one of the groups, we used the degree parameter as a measure of node importance because betweenness parameter could not be calculated). 3) Brokers’ importance: Brokers of each group were left behind intentionally. 4) Random: Family group (50% of individuals) were randomly chosen for reintroduction. To assess the impact of the “removal” of nodes we used three network metrics: number of network components, number of network. largest components, and the number of isolates nodes. Metric values were obtained using the *statenet* package. Random individuals and networks plots of the different scenarios were performed in R (R Core Team, 2013).

5.5 RESULTS

5.5.1 Hierarchy and network structure

Dominance networks in the Floreana mockingbirds did not contain cyclic triads ($P_t = 1$; $t_{tri} = 1$), Furthermore, this result was not significantly different from the simulated networks ($p_{combined} > 0.05$).

We found that the main factor explaining the dominance interactions in the Floreana mockingbird was age related (Fig. 5.2). The negative coefficient for selective-mixing in age (Table 5.1) indicated that older individuals tended to interact aggressively with younger individuals. Meanwhile for the actor effect of age, the negative coefficient (Table 5.1) indicates that young individuals were less likely to initiate dominance. We did not find any significant effect of reciprocity, sexual homophily, or body size difference. MCMC did not show any signs of model degeneracy. Furthermore, the simulations of the modelled network were similar to our observed network, corroborating the fit of our model (Table 5.2).

5.5.2 Harvesting scenarios

The removal of nodes with different importance in the social network structure affected the number of components and isolates (Table 5.3, Fig. 5.3). From the four simulations, scenario 3 (removal of brokers) had a predominant effect in the structure of the social network compared with the observed network.

5.6 DISCUSSION

We conclude that hierarchy structure in CB animals was important to the dynamics of both individual and group stability levels (Cant, English, Reeve, & Field, 2006; Ellis, 1995; Williamson, Lee, & Curley, 2016). Here, we show that Floreana mockingbird family groups form transitive (linear) relationships. Our findings are similar to other CB animals where transitivity methods have been used (Dey & Quinn, 2014; Dey *et al.*, 2013). This transitiveness is expected due to the difference in individual attributes that establish dominance ranks and resources accessibility, and self-organization (Chase & Seitz, 2011).

Regarding the structure of the social networks, from the eight factors we hypothesized as explanatory of the network structure, only two appear to explain the dynamic of dominance in the Floreana mockingbird family groups. These two factors are explained by individual attributes related with age. Age has been stated as the main predictor of social status in the Floreana mockingbird and in the Galápagos mockingbird (*Mimus parvulus*) (Curry, 1988a). In the Galápagos mockingbird, older individuals display dominance relationships with younger individuals even in the same-age cohort (Curry, 1988a). Similarly, age is related to reproductive state and dominance in breeding groups of the facultative CB white-breasted thrasher (*Ramphocinclus brachyurus*) (Temple *et al.*, 2009), in pied babblers (*Turdoides bicolor*) where older individuals dispersing are more likely to gain a breeding position as dominants (Raihani, Nelson-Flower, Golabek, & Ridley, 2010), and in long-tailed tits (*Aegithalos caudatus*) where age and size are related to dominance in hierarchy position within the group (Napper, Sharp, McGowan, Simeoni, & Hatchwell, 2013).

Considering the correlation between age and social status, we found that the probability of link formation increased when the social status decreased. Older individuals engage more in dominance with younger individuals than with other older individuals (differential homophily by age). Aggressive interactions from dominant to subordinate are the main trait of strictly linear hierarchy relationships (Shizuka & McDonald, 2012) and normally occur in Galápagos mockingbirds (Grant, 1983), and other CB systems, as a way of keeping the reproductive skew towards dominant individuals and subordinates in reproductive suppression (Brouwer *et al.*, 2009; Taborsky, 1985; Williams, 2004; Young *et al.*, 2006). This is supported by our non-significant results on reciprocity, we found that aggression is unidirectional from dominant individuals to subordinates. Contrary to our hypothesis, we did not find any effect of size and sex on the structure of the social network. In some CB species phenotypic traits such as plumage coloration (Cockburn, Osmond, Mulder, Double, & Green, 2008) and body size (Napper *et al.*, 2013; Spong, Hodge, Young, & Clutton-Brock, 2008) are predictors of dominance. Although, we did not find any significant effect in the aggression between same-sex dyads (sexual homophily) our positive coefficient indicates that dominance was more likely to occur towards the opposite sex. In other CB systems, aggression by sexual homophily is explained by intrasexual competition for a breeding position inside the groups (Dey & Quinn, 2014; Dey *et al.*, 2013; Mitchell, Jutzeler, Heg, & Taborsky, 2009). In Floreana mockingbirds, group structure has not yet been studied in detail, but for the conspecific Galápagos mockingbird (*M. parvulus*), dominance occurs across sexes; females are subordinate to males and female dominance over other females is associated with the rank of the female's mate (Curry, 1988a).

The dominance pattern we observed between sexes may be associated with the sex ratio of the population (Chapter 2) and the use of a plural CB strategy. Plural CB occurs when more than one female reproduces inside the family group or when multiple females share the same nest (Cockburn, 2004). Unlike the other two Galápagos mockingbirds (*M. parvulus* and *M. macdonaldi*) which display plural CB more often (Curry, 1988a; Von Lippke, 2008), Floreana mockingbirds do not display it frequently (Curry, 1988a). The rarity of this strategy might reduce the frequency of intrasexual competition because, in non-plural breeding groups, all the members are closely related (Grant *et al.*, 2000). Another factor that might explain our non-significant effect of sex, is that the behavioural observations of our study happened during the non-breeding season when family groups in the Floreana mockingbird are less compact (Ortiz-Catedral unpublished). In some social animals, the social network structure changes with reproductive stage (Dey *et al.*, 2015; Patriquin, Leonard, Broders, & Garroway, 2010). For example, in non-breeding long-tailed tits, groups do not occupy stable and exclusive territories (Hatchwell, Anderson, Ross, Fowlie, & Blackwell, 2001), and kinship is the main factor that determines group cohesion and decreases aggressiveness between group members (Napper & Hatchwell, 2016). A temporal dominance network stability study would explain whether aggressive interactions between sexes vary with breeding and non-breeding seasons for the Floreana mockingbird.

Finally, we demonstrated that the removal of individuals in social species can affect the social dynamics, network stability and reproductive behaviour. A similar effect has previously been shown in colonial bats (*Myotis septentrionalis*) using simulated removal of multiple roosting sites, resulting in network fragmentation increasing linearly with the proportion of roosting sites removed (Silvis, Ford, Britzke, & Johnson, 2014). In this study, when the roosting sites were physically removed, behavioural changes were observed at a colony level (Silvis, Ford, & Britzke, 2015). In CB pukekos (*Porphyrio melanotus melanotus*), after the culling of individuals for population management, the remnant groups experience an increase of clutch size associated with the disruption of social groups (Hing, Healey, Dey, & Quinn, 2017). This increase might be explained by the communal nesting characteristic of pukekos, where all the breeding females lay eggs in the same nest simultaneously (Craig & Jamieson, 1990), in an scenario where isolated females from disrupted groups join existing groups instead of establishing new ones. For the CB fish *Astatotilapia burtoni*, the removal of dominant individuals results in social instability and competition for territories (by social ascent and territory expansion); some subordinate fish become dominants, or neighbouring groups take over territories after dominants are removed (Piefke *et al*., 2021). Our simulations support the hypothesis that the removal of individuals by inadequate harvesting selection will create a network disruption, thus impacting the success of the reintroduction. The number of components and isolates of our networks tend to increase with the removal of individuals, especially in scenario 3 with the removal of brokers; brokers have been suggested as an important weakness in network structure and are usually targeted for removal when the purpose is the collapse of criminal social networks (Duxbury & Haynie, 2018; Wood, 2017). It is unsurprising that the removal of targeted individuals often has a strong effect on the stability of social networks. For example, the removal of random individuals in a simulated social network of killer whales (*Orcinus orca*) was more stable than the removal of targeted individuals who mimicked real-life captures (Williams & Lusseau, 2006). While some social animals show resilience in connectivity after the removal of random nodes (Naug, 2009), highly hierarchical networks are more prone to collapse because individuals may have specific roles within a network. For instance, in captive groups of Rhesus macaques (*Macaca mulatta*), social collapse of the groups was observed shortly after the removal of alpha males (Beisner *et al.*, 2015).

5.6.1 Conservation remarks

The Floreana mockingbird is a target species for the reintroduction to Floreana Island into the Floreana Island restoration project (Ortiz-Catedral, 2018). Based on our analyses, we strongly encourage that harvesting of mockingbirds for reintroductions requires the movement of entire family groups, rather than being based on individuals as is suggested by Bozzuto *et al.* (2017), who recommended harvesting a limited number of individuals to maintain the population source. We believe that the current population of Floreana mockingbird could cope with the harvesting of family groups due to helpers in CB systems providing a pool for replacement of breeders, where the recruitment of new individuals increases with the space available left by missing individuals (Walters, Cooper, Daniels, Pasinelli, & Schiegg, 2004) (Chapter 3). Family group harvesting could act to keep social cohesion and avoid group disruption. When planned correctly, this could increase the probability of establishment and reproductive success, because of the presence of a pre-existent social structure which can facilitate social stability after a translocation (Snijders *et al.*, 2017). Avoiding group disruption should be a priority task, because disruption leads to the appearance of floaters which, in other CB species, have reduced life expectancy. For example, an experiment in pied babblers (*Turdoides bicolor*) showed that individuals that became floaters suffered a loss of body mass because they invest more time in vigilance against predators and less feeding compared to when they were in a group (Ridley, Raihani, & Nelson-Flower, 2008).

The lack of inclusion of aspects of sociality might explain the high rate of failure in translocations of CB birds, which have focused on the movement of specific ages classes instead of moving entire groups (e.g. Cox & McCormick, 2016; Groombridge *et al*., 2004). Here the principal outcome was the disruption of the social system, with birds becoming social pair breeders without helpers during the first stages of the translocation (Armstrong, Lovegrove, Allen, & Craig, 1994; Carrie, Conner, Rudolph, & Carrie, 1999; Komdeur *et al*., 1995; Mumme & Below, 1999). To the best of our knowledge, only two cases of translocations of CB birds did not lead to social disruption. This might be explained by the fact that birds were moved as entire family groups in the case of the brown treecreeper (*Climacteris picumnus*) (Bennett, Doerr, Doerr, Manning, & Lindenmayer, 2012) and because the species displayed plural breeding in the case of the black-eared miner (*Monarina melanotis*) (Clarke *et al*., 2002). Although there are no mockingbird translocations reported yet, there is a case of a population of CB tropical mockingbirds (*Mimus gilvus*) resulting from a release of captive birds in Panamá (Chapman, 1941). Tropical mockingbirds are facultative cooperative breeders and although the hypothesis of how this population developed CB are unanswered (Morton, Stutchbury, & Piper, 2004) this case presents an optimistic scenario for the Floreana mockingbird reintroduction.

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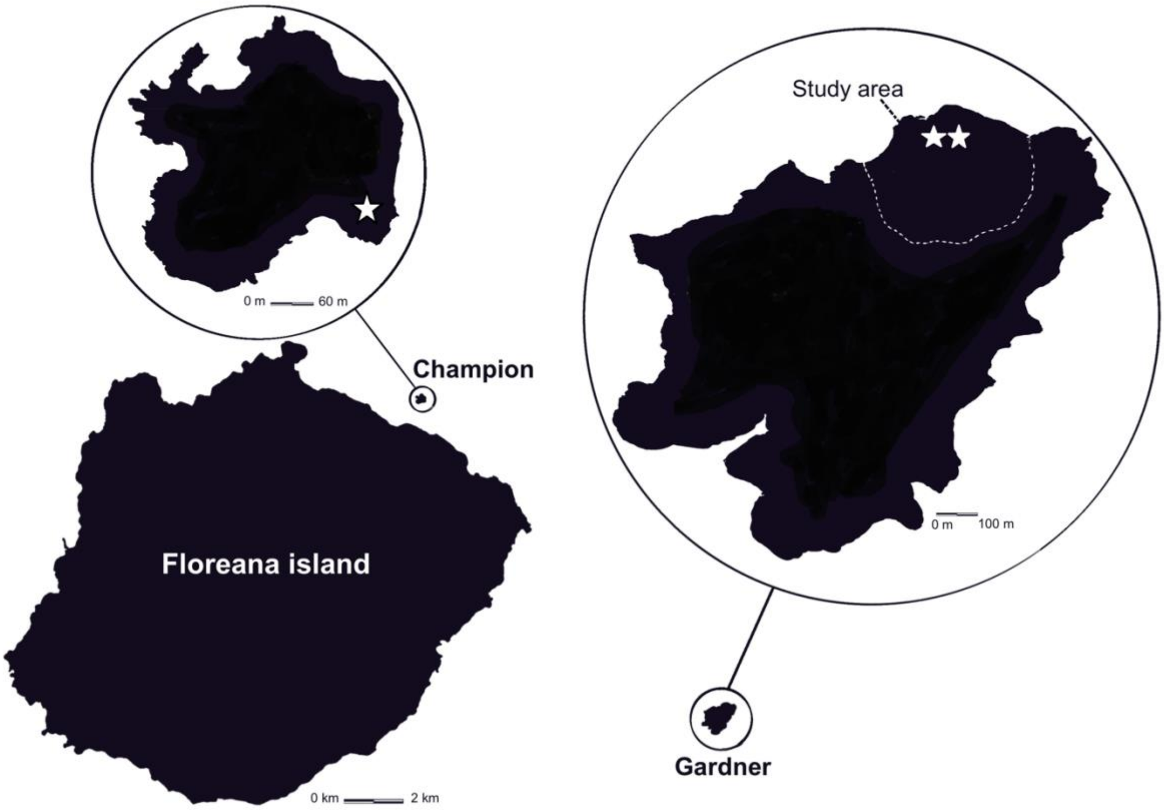

Figure 5.1 Location of the islets of Champion and Gardner-by-Floreana. Dotted area in Gardner represent the monitored area by the project on this islet. Stars represent the approximate position of the groups studied.

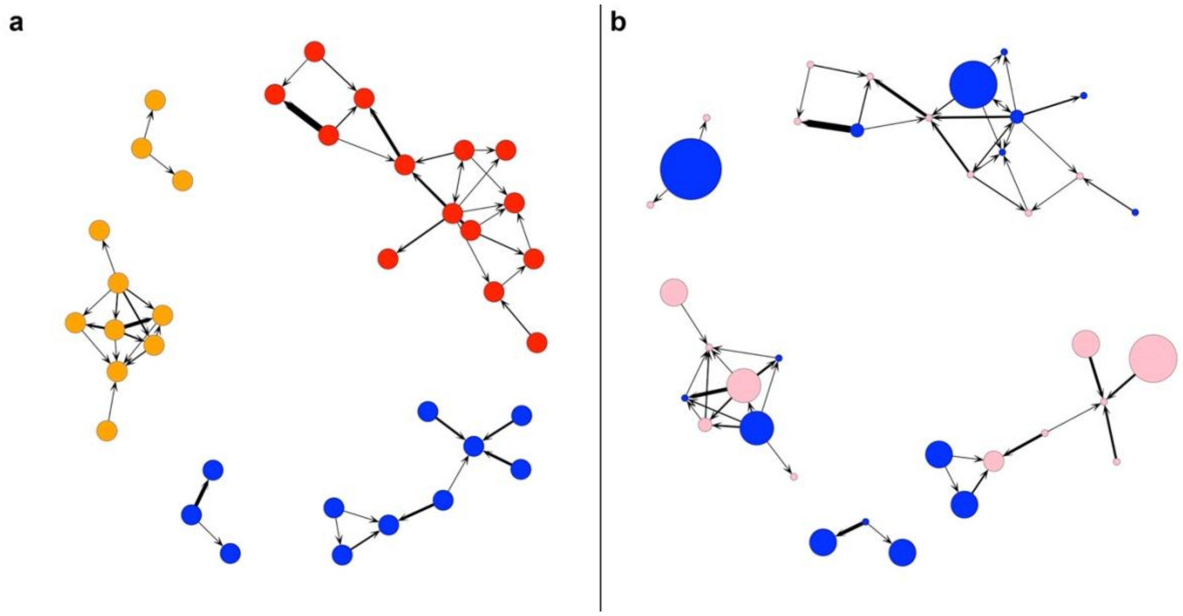

Figure 5.2 Networks of dominance display of the Floreana mockingbird. Networks are displayed by a) family group by colour and b) by sex (blue nodes represent males and pink nodes represent females) and age (node size was scaled to the age of the individuals) where large nodes represent older birds and smaller nodes represent young birds. Tie thickness represents the number of interactions between nodes and arrows represent directionality of the interaction. Figures were created using *statnet* package.

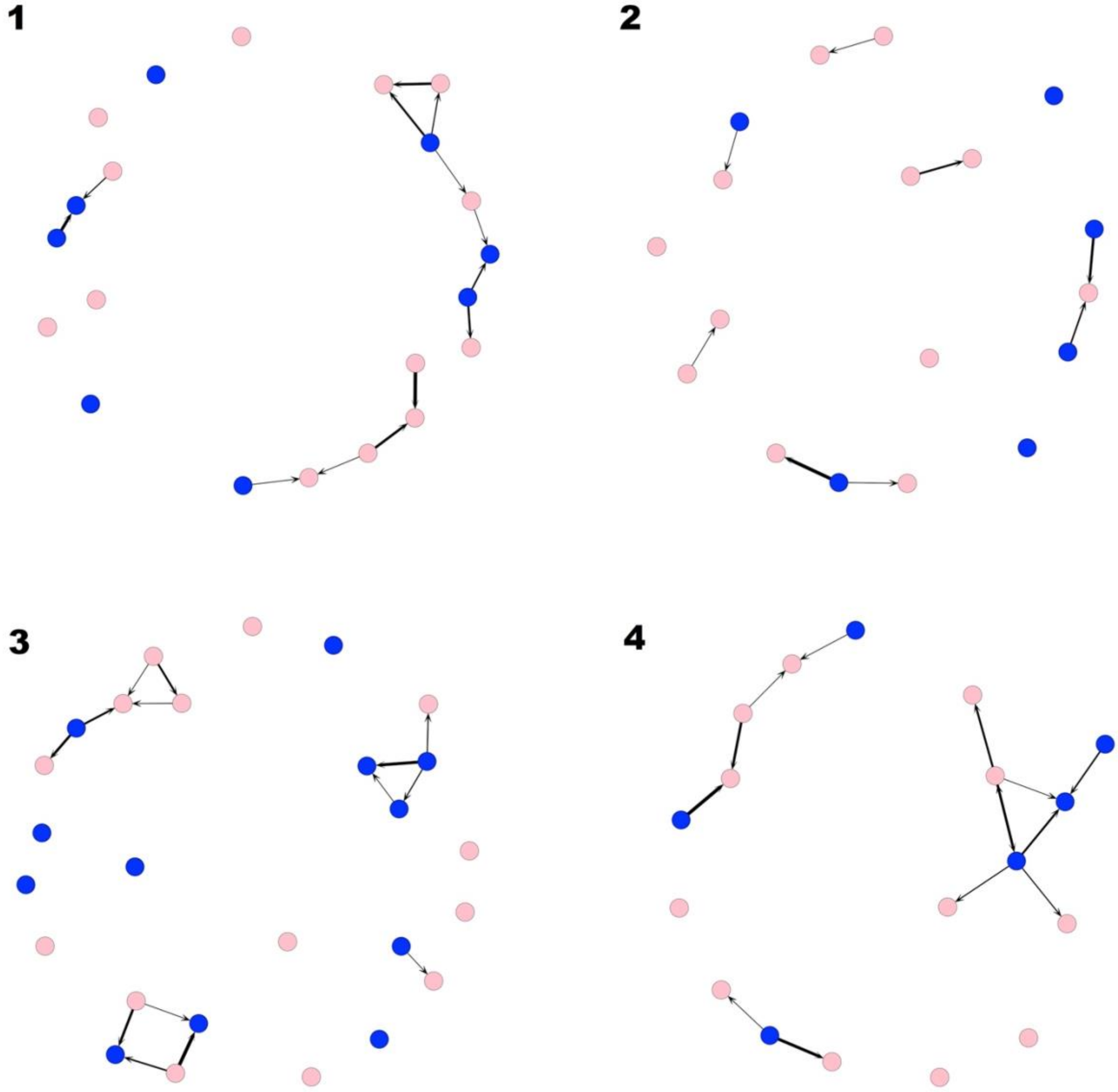

Figure 5.3 Different scenarios of simulated harvesting for translocations after removal of individuals: 1) With older individuals in the translocation. 2) Without nodes with centrality importance. 3) Without brokers and 4) Randomly selected. Birds displayed by sex from the original social network of figure 5.2a. Colour of the nodes represents the sex of the individuals as stated in figure 5.2b.

Table 5.1 Terms and estimates from the ERGM fit of a Floreana mockingbird dominance network.

Model term	Estimate	SE	P value
Sum	0.99	0.27	**0.0002**
Nonzero	-3.58	0.31	**<0.0001**
Actor effect of Sex (male)	-0.08	0.81	0.33
Sexual homophily	0.09	0.11	0.39
Age homophily	-0.55	0.16	**0.0007**
Difference in body size	-0.09	0.10	0.40
Actor effect of age	-0.16	0.51	**0.001**
Receiver effect of age	-0.01	0.03	0.63
Reciprocity	-0.25	0.20	0.20

Table 5.2 Statistical parameters from the observed and the mean statistical parameters of the simulated networks.

	Networks	
Parameters	Observed	Simulated
Sum	119.0	114.7
Non_zero	50.0	49.1
Node_factor sex	98.0	99.0
Node_match sex	63.0	61.5
Node_match age	30.0	31.4
Abs_dif size	69.1	68.9
Node_icov age	186.0	184.5
Node_ocov age	350.0	311.5
Mutual	-115.0	-108.5

Table 5.3 Impact of node removals by different harvesting simulations on the structure of the observed social network.

	Components	Largest component	Isolates
Observed	5	14	0
Scenario 1	9	7	6
Scenario 2	10	6	4
Scenario 3	26	5	11
Scenario 4	6	6	3

Chapter 6

General conclusions and management recommendations

Fledging of Floreana mockingbird, Champion Islet, 2017

Photo: Sabina Ascencio Ramirez

6.1 GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In this final chapter, I review evidence from the previous chapters with the aim of addressing management questions regarding the future of the Floreana mockingbird. The analyses presented in this thesis address some of the most important research priorities for the species that should help with accurate management planning that ensures the success of the future reintroduction of this species to Floreana Island.

Before any ecological or behavioural questions can be answered, some basic life-history aspects of a species require investigation. Accurate sexing of individuals is one of the most fundamental tools for the study of ecology. Sex identification can help answer questions regarding ecological and behaviour segregation (Catry, Phillips, Croxall, Ruckstuhl, & Neuhaus, 2006), and accurately determine the sex ratios of populations that can influence conservation actions in endangered species (Brekke, Bennett, Wang, Pettorelli, & Ewen, 2010). In addition, non-invasive methods are useful when monitoring endangered birds that might be susceptible to changes in stress levels (Groombridge *et al.*, 2004). The development of non-invasive sex identification tools needs to be the first milestone when planning the study and conservation of an endangered species whose life history is unknown, to minimize any disturbance that could have a negative impact on the ecology of the species (Reddy, Prakash, & Shivaji, 2007). For the Floreana mockingbird, this tool was one of the gaps that needed to be addressed. In this thesis, using a combination of morphometric measurements, molecular techniques and statistical analysis, I developed a non-invasive method for the accurate sexing of the Floreana mockingbird (Chapter 2). Previously we used morphometric measurements of the conspecific and more common Galápagos mockingbird (*Mimus parvulus*) as a basis to infer the sex of the Floreana mockingbird (Curry, 1988, 1989; Curry & Grant, 1989; Kinnaird & Grant, 1982).

Throughout this thesis, I used ecological references to the Galápagos mockingbird as a proxy for comparison with the Floreana mockingbird, as it is one of the most studied mockingbirds in the Galápagos and data are widely available. However, the use of morphological measurements of one species to assume the sex of another could create bias that might impact the results of future research and/or management actions, especially when a difference in morphological trait has been already described (Grant, Curry, & Grant, 2000) and when dealing with an endangered species (Reddy *et al.*, 2007). In addition, the non-invasive nature of the method for sexing that I developed here, is simple, allowing anyone with basic ornithological skills to apply it on this species without a statistical background. This is a small but significant part of the planning and development of the reintroduction process and conservation of the Floreana mockingbird, as the management of the species is undertaken primarily by personnel of the Galápagos National Park, who generally do not have an academic understanding of statistical methods and discriminant analysis formulas. Moreover, individuals working with these birds spend limited time in the species' habitat because of the remoteness and relative inaccessibility of the islets. Having a threshold for wing measurement for males and females will reduce unnecessary handling time and the use of invasive methods such as the removal of feathers or blood sampling for molecular sexing, and will improve the understanding of the ecological dynamics of this species.

In addition to the issue of tools for reliably and accurately determining the sex of these birds, one of the most important research priorities stated by the IUCN for the Floreana mockingbird is the status of the population trend. In Chapter 3, I described, for the first time, the population trend of both islets using robust methods (obtained through years of banding) of capture-mark-recapture models. Furthermore, I estimated several vital parameters previously unknown for the species that will help in the development of population viability analysis (PVA). The use of PVAs will facilitate the assessment of the extinction risk of this species under different scenarios of conservation and harvesting strategies for any reintroduction (Johnson & Greenwood, 2020). Although out of the scope of my PhD, nevertheless, it is a research area that I hope to undertake in the future.

The results presented in Chapter 3 have ended years of speculation and underestimations of the number of remaining Floreana mockingbirds (e.g. Jiménez-Uzcátegui, Llerena, Milstead, Lomas, & Wiedenfeld, 2011). Moreover, the results show that despite the general lack of intensive conservation action (apart from habitat protection), the ongoing access restriction to the islets has likely contributed to a population of ~1000 individuals. This new estimate has supported the reclassification of the species from critically endangered to endangered in 2017 (BirdLife International 2021). Although the influence of rainfall is well known for other land-birds in Galápagos (Curry, 1985; Grant, Grant, Keller, & Petren, 2000; Wingfield *et al.*, 2018), my research further corroborates current understanding of the association between the survival of individuals and rainfall across the islands. As I have stated here, and has been noted by other researchers (Dueñas, Jiménez-Uzcátegui, & Bosker, 2021; Wiedenfeld & Jiménez-Uzcátegui, 2008), the population is vulnerable to prolonged droughts that are expected to increase in intensity and frequency as a result of climate change (Cai, Santoso, *et al.*, 2015; Cai, Wang, *et al.*, 2015).

Taking this negative outlook into account, I believe it is time that a more proactive conservation approach is undertaken to ensure the long term viability of the populations. Firstly, despite my research showing an optimistic scenario overall in the population trend of the mockingbirds, I did find a slight decrease in the growth of the Gardner population. Standardization and improvement of the methodology of monitoring in this population will allow the use of more specialized models of capture-mark-recapture that might help to answer the causes of the decreasing population growth. Secondly, I support the reintroduction plan designed for the species which will be implemented when invasive mammals are eradicated from Floreana Island (Ortiz-Catedral, 2018). In this plan, I particularly support the use of individuals of both populations to create a third population on Floreana; the aim of using individuals of both populations is to improve the genetic diversity of the species (Bozzuto, Hoeck, Bagheri, & Keller, 2017). In theory, the exchange of genes between populations should be straightforward, moving the population away from the negative effects of a bottleneck. But in practice, mixing individuals of different populations is more complex than it looks, especially when working with species with complex vocalizations and social structures such as the Floreana mockingbird. I would encourage conservationists and practitioners to incorporate behavioural aspects in the reintroduction plan, with the aim of avoiding any behavioural problems that might otherwise interfere with the success of the reintroduction. I have described these aspects in this thesis and expanded on this topic below.

Since the first translocations of kakapo (*Strigops habroptilus*) and kiwi (*Apteryx spp.*) in New Zealand in the late 1800s (Hill & Hill, 1987) there have been several reintroductions worldwide with different levels of success, as summarized in Chapter 1. All reintroductions have specific challenges, but reintroducing birds that express vocal differences, and those species that are highly social, has their own issues. As explained in the introduction of Chapter 4, vocal divergence and its impact on the viability of the population of endangered species is a recent matter of study in conservation biology (Ryan, 2006). Dialects can naturally arise when populations are isolated by natural barriers (Podos & Warren, 2007), but they can also result from conservation actions that intentionally create a divergence in vocal cultures, for example, in parrots (Martínez & Logue, 2020) and honeyeaters (Crates *et al*., 2021). Difficulties related to the cultural divergence between populations has happened even in New Zealand, one of the countries with a high incidence of successful reintroductions. Cases like the North Island kokako (*Callaeas wilsoni*) (Bradley, Molles, & Waas, 2014) and the North Island saddleback (*Philesturnus rufusater)* (Parker, Anderson, Jenkins, & Brunton, 2012) are some of the most well-known examples from which we are able to learn more. With this in mind, I considered what might happen if conservation management of mockingbirds tried to combine individuals of different populations to create genetically diverse populations; how likely is it that individuals from different populations recognise each other as potential mates? In this thesis, I described the first step to address this question (Chapter 4) and I conducted the first study based on a behavioural ecology approach that links to the conservation of the species.

I investigated whether the vocalizations between populations were different, and I identified the possible parameters causing that difference. I discovered a cultural difference between populations that might be explained by a combination of several factors including a morphological difference and the effect of cultural evolution by drift. These factors might be intensified due to the isolation of the populations after the extinction of the main population on Floreana Island. Moreover, my results in Chapter 4, might appear negative and could possibly delay the attempt of the reintroduction until further studies are done. My findings on this topic provide a source of several research questions and opportunities for research for future conservationists taking the lead in the project. I would recommend starting with experimental playbacks that assess responses to the vocalisations of each population and the recognition of dialects and the potential for assortative mating or aggressive behaviour between individuals of different populations. With the findings of this chapter, I encourage the incorporation of behavioural factors, in addition to the narrow genetic approach of previous studies on the Floreana mockingbird, when planning future reintroductions.

As mentioned above, before this thesis, behavioural components has not been considered in planning reintroductions of this species. At this stage, the reintroduction plans and research highlight the importance of moving individuals from the two populations to Floreana but do not detail the precise methodology that will be used. The most relevant plan for translocating individuals from the islets to Floreana was elaborated by Bozzuto *et al.* (2017) who described several scenarios of harvesting for reintroduction which did not consider the social organization of the species and assumed the birds are socially monogamous rather than cooperative breeders. Unfortunately, this is not an isolated case but is more the accepted method for most of the translocations attempted for cooperative breeding birds; moving birds as individuals instead of as a social group. In Chapter 5, I quantify the probability of social collapse of mockingbird groups by simulating different scenarios of reintroductions where more than two birds are taken for harvesting. Answering the social collapse questions before exploring some of the patterns that explain the social dynamics of the Floreana mockingbird groups would be nonsensical. Therefore, in Chapter 5, I described the transitive nature and social structures of mockingbird family groups. Consistent with previous research carried out on other mockingbird species in the Galápagos, I found strong hierarchical dominance relationships within Floreana mockingbird groups. Moreover, I found that one of the main factors explaining the structure of the social dynamics in the groups I studied were related to age, and consequently, social status. However, this information has been previously documented for this species but using different methodologies (Curry, 1989). My research on this topic is the first time that a statistical method, normally used in the social sciences, has been applied to the Floreana mockingbird; an accurate method that has been used in another cooperative breeding species (Dey & Quinn, 2014; Dey, Tan, O’Connor, Reddon, & Caldwell, 2015). Nevertheless, the highlight of Chapter 5 is the use of the information on the social structure to simulate different scenarios of social collapse if family groups are considered units for reintroduction purposes. Ideally, a simulation built using data from different breeding and non-breeding seasons would be more robust, however, my data were constrained by the global circumstances of the COVID-19 pandemic, hence and only reflecting the social dynamic of the non-breeding season of the mockingbirds. I would recommend the continuation of the study of social dynamics during a different time of the year and throughout successive years with the aim of identifying if interactions are stable across time. Finally, based on the information generated in this chapter and the only information available regarding the sociality of the Floreana mockingbird, I do encourage that the movement of the species by harvesting be done by family groups instead of randomly chosen individuals. As I discussed in Chapter

5, a social rupture could decrease the probabilities of establishment and reproductive success in a newly translocated population. Furthermore, using the information generated by the study of the social dynamics of the mockingbirds, I suggest the implementation of experimental translocations using surrogate species; species of least concern but with similar ecology. For example, the moving of groups of Galápagos mockingbirds (*M. parvulus*) from Santa Cruz Island to North Seymour Island, where they are locally extinct, or movement of groups of long-tailed mockingbirds (*M. longicaudatus*) on mainland Ecuador.

The evidence and analysis I have provided in this thesis will help forge a better understanding of selected ecological and demographic aspects of the Floreana mockingbird that might help in the planning and success of its translocation to Floreana Island. Floreana Island has been one of the most impacted islands in the Galápagos archipelago due to being the first colonized by humans and has subsequently lost many species compared with other populated islands within the archipelago (Dvorak *et al.*, 2017; Jiménez-Uzcátegui & Ortiz-Catedral, 2020). Recent interest in restoring Floreana has been emerging, categorizing it as one of the islands where it is feasible to eradicate invasive species (Holmes *et al.*, 2019). This interest has created multiple opportunities for several NGOs and universities, who are working alongside the Galápagos National Park attempting to restore Floreana as has been done with other islands in the archipelago. The huge challenge and main difference is that Floreana would be the first inhabited island in the Galápagos subject to an eradication attempt. The Floreana mockingbird has huge relevance in the history of science as it is one of the species that inspired Charles Darwin and his theories about evolution and speciation. Some researchers have given the species the nickname “Darwin’s muse” (Hoeck *et al.*, 2010). I think the species could become the flagship of the restoration of Floreana and a cornerstone of the conservation on the Galápagos. In addition to conducting the research needed and suggested by this thesis, a parallel conservation project is recommended to focus on increasing human engagement and a better understanding of this work. A project involving the local population of Floreana in a social/conservation campaign could increase support for the eradication of invasive species and for the future reintroduction of the mockingbirds. This approach will also benefit other species endemic to Floreana (at risk of local extinction or no longer present on the islands) such as the Floreana race-snake (*Pseudalsophis biserialis biserialis*) and the Medium-tree finch (*Camarhynchus pauper*).

Throughout the time I took to complete this thesis, I have engaged in several campaigns that increased the awareness of this species, although most of these were internationally focused rather than orientated to the local Floreana population. I participated in an educational campaign for Education New Zealand in 2019 and in a Nature documentary series featuring the current research on the Galápagos Islands by Channel 4 in the United Kingdom (Appendix 2), a programme that has been broadcast in several English speaking countries. Moreover, during my participation as a volunteer and later as PhD student on this project, I was able to train several park rangers from the Galápagos National Park in basic ornithological skills such as trapping, banding and taking morphological measurements of the Floreana mockingbird (Appendix 3), which will help the development of autonomous monitoring by personnel of the Galápagos National Park. In addition, while conducting my research I have been able to participate in other research projects with the mockingbird and other Galápagos species (Appendix 4). Finally, this thesis has been structured as a thesis by publication in peer review journals, with two of the journals selected displaying abstracts in Spanish. Finally, to improve the democratization of this information, I also plan to publish science communications articles (which I began during my last year of study) with non-technical language in both

English and Spanish. This will enable the spread of information to conservation practitioners and supporters outside the academic world who do not have access to academic information and/or are in places where English is not the first language.

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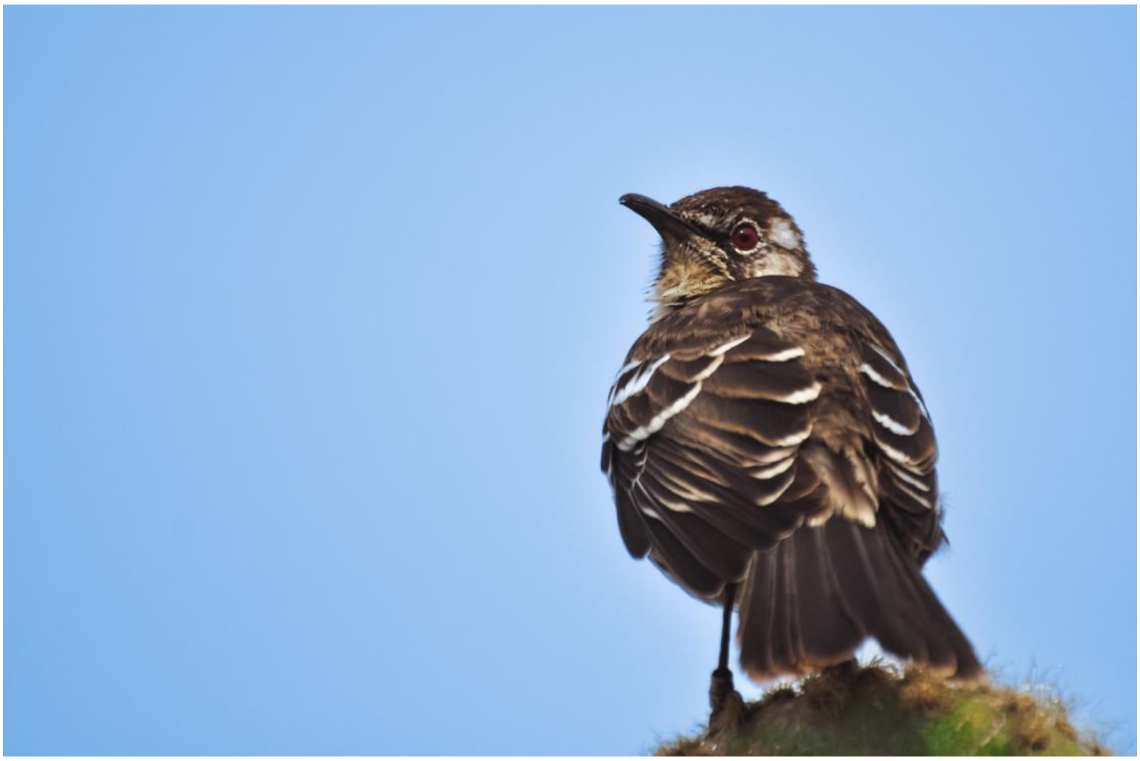
7 Appendices



Floreana mockingbird, Gardner Islet.

Enzo M. R. Reyes

7.1 APPENDIX 1

Photography of the Galápagos Islands and islets including the habitat of the study area.

Figure 0.1 Galápagos archipelago with the location of Floreana Island at the south-centre of the archipelago. Imagen: USGS-LandLook© 2021

Figure 0.2 Close up of Floreana Island with its islets, Champion in the northwest and Gardner in the southwest. Imagen: USGS-LandLook© 2021

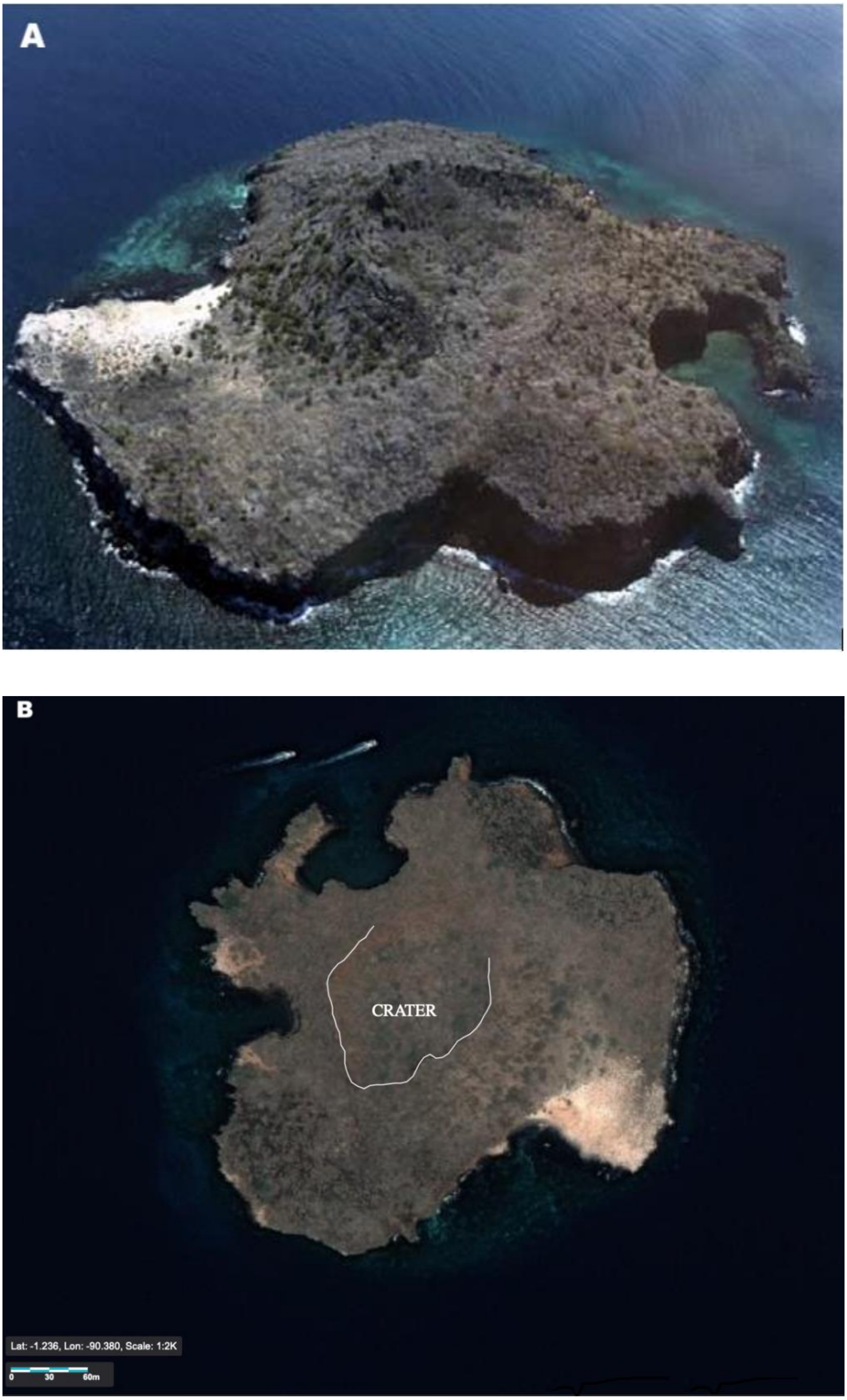

A
B
CRATER
Lat: -1.236, Lon: -90.380, Scale: 1:2K
0 30 60m

Figure 0.3 A) Aerial view from Champion Islet. Photo: Heidi Snell. B) Satellite image of Champion with the location of its crater. USGS-LandLook© 2021. C) Floreana mockingbird on Champion Islet. Photo: Enzo Reyes. D) Habitat structure on Champion Islet. Photo: Luis Ortiz Catedral.

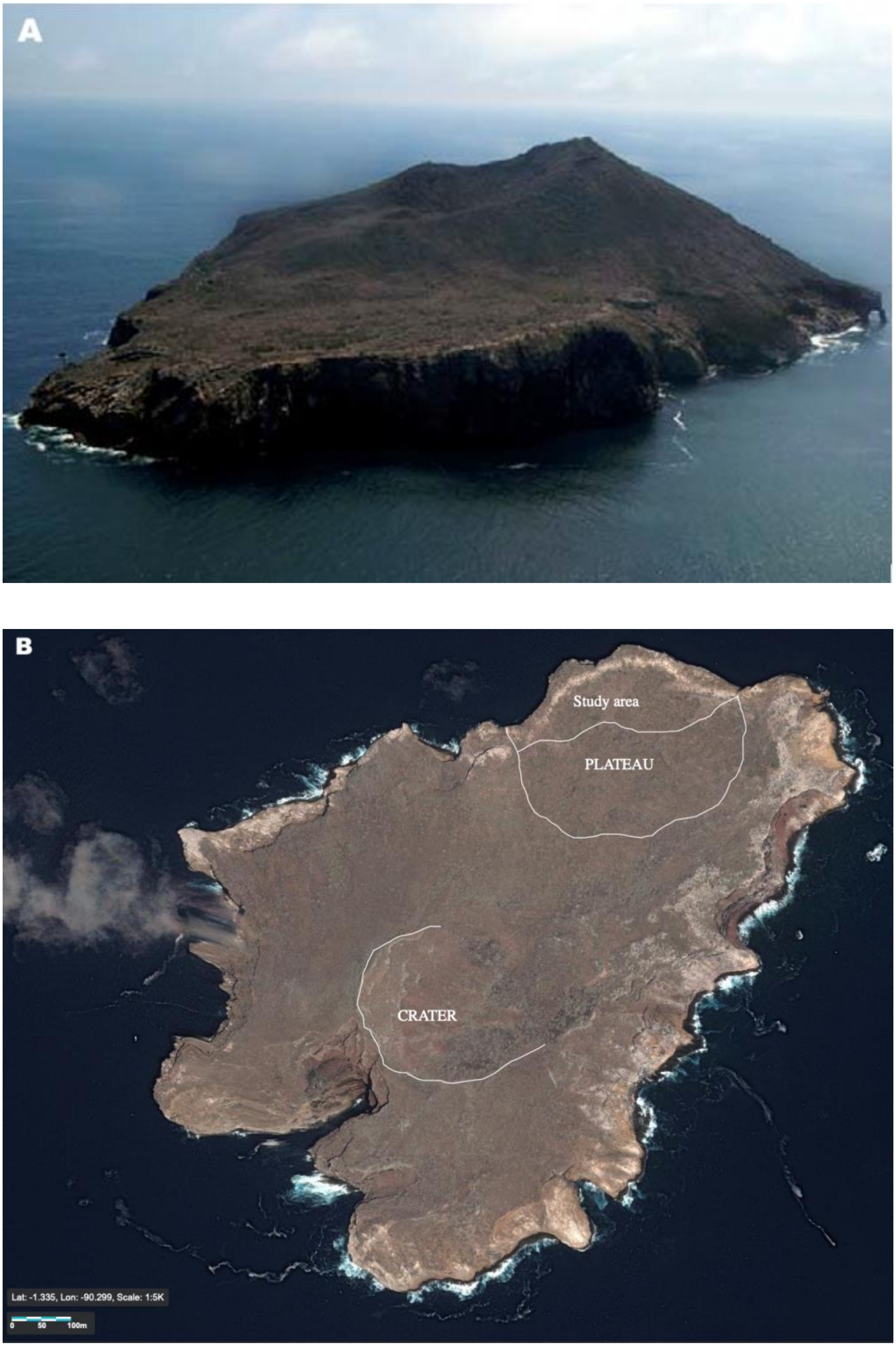

A
B
Study area
PLATEAU
CRATER
Lat: -1.335, Lon: -90.299, Scale: 1:5K
0 50 100m

Figure 0.4 A) Aerial view of Gardner-by-Floreana Islet. Photo: Heidi Snell. B) satellite image of the islet showing the location of the crater and study area inside of the plateau. USGS-LandLook© 2021. C) Floreana mockingbird on Gardner Islet. Photo: Enzo Reyes. D) Habitat structure on Gardner Islet. Photo: Luis Ortiz Catedral.

7.2 APPENDIX 2

Figure 0.5 Footage of the documental series “*My Family and the Galápagos*” Series 2 episode 3 by Channel 4 from the United Kingdom available at: https://www.channel4.com/programmes/my-family-and-the-Galápagos/on-demand/69777-003

Because it was the bird that inspired Charles Darwin's theories about evolution on his expedition

7.3 APPENDIX 3

Figure 0.6 Training park rangers from the Galápagos National Park on bird banding skills.

Photo: Sabina Ascencio Ramirez.

7.4 APPENDIX 4

Papers published and accepted of other research related to the Galápagos:

A) *Herpetology Notes*, Volume 12 (2019).

Herpetology Notes, volume 12: 701-704 (2019) (published online on 02 July 2019)

Diet of six species of Galapagos terrestrial snakes (*Pseudalsophis* spp.) inferred from faecal samples

Luis Ortiz-Catedral[1,*], Eli Christian[1], Michael John Adam Skirrow[1], Danny Rueda[2], Christian Sevilla[2], Kirtana Kumar[1], Enzo M. R. Reyes[1], and Jennifer C. Daltry[3]

The Galapagos terrestrial snakes, or 'Galapagos racers' (*Pseudalsophis* spp.) are a monophyletic group of nine species within Dipsadidae, exclusively found in the Galapagos Islands (Zaher et al., 2018). A single continental species, *P. elegans*, is the closest relative of these island species (Zaher et al., 2018), and is found from Ecuador to Chile (Armendáriz, 1991; Carrillo de Espinoza and Icochea, 1995; Thomas, 1977). The group has been the subject of various taxonomic reviews since the early 1900s (Thomas, 1997). Although there have been significant advances in understanding the evolutionary history of the group and their phylogenetic affinities (Grazziotin et al., 2012; Zaher et al., 2018), basic aspects of their biology have remained largely undocumented, in particular the diversity of prey consumed by the different species across the Galapagos archipelago and mainland South America. For instance, in the 106 years since VanDenburg's (1912) first account of food items in the stomach contents of Galapagos racers, there have only been five studies that describe prey species for these snakes, which report: lava lizards (*Microlophus* spp.) (Altamirano, 1996; Merlen and Thomas, 2013; Cadena-Ortiz et al., 2017); marine iguana (*Amblyrhynchus cristatus*) hatchlings (Laurie and Brown, 1990; Merlen and Thomas, 2013); land iguana (*Conolophus subcristatus*) hatchlings (Werner, 1983); and coastal fishes (*Bolinichtys longipes*, *Dialommus fuscus* and *Labrisomus denditricus*) (Merlen and Thomas, 2013). There are also unpublished reports of Galapagos racers ingesting large painted locusts (*Schistocerca melanocera*) (Jackson, 1993), and three observers (park rangers from the Galapagos National Park) have witnessed *P. dorsalis* ingesting eggs of Galapagos doves (*Zenaida galapagoensis*) on Santa Fe Island (G. Quezada, M. Gavilanes and C. Gaona pers. comm.). There is even an unconfirmed report of a terrestrial snake ingesting the fruit pulp of bitter melon (*Mormodica charantia*) on Santa Cruz Island (Olesen et al., 2018), but it is unknown whether the snake ate the bitter melon deliberately or by accident (e.g. while preying on a small vertebrate associated with the fruit). To contribute to the knowledge of the feeding ecology of Galapagos racers, and to shed light on the biology of these poorly studied reptiles, we conducted a field study on the prey diversity of six species at nine localities in the Galapagos Islands from 2015 to 2018. We examined 79 faecal samples opportunistically collected in the field during our ongoing studies on the morphological variability of Galapagos racers and, in particular, the demographics of Floreana racers (*P. biserialis biserialis*). Furthermore, we report eight predation events observed in the field at two locations for two species.

We captured racers and conducted field observations, on the following islands: Seymour Norte (0° 23' 30" S, 90° 17' 0" W); Santa Fe (0° 49' 0" S, 90° 3' 30" W); Fernandina (0° 22' 0" S, 91° 31' 20" W); Rabida (0° 24' 35", 90° 42' 30" W); Santiago (0° 15' 30" S, 90° 43' 30" W) and Pinzon (0° 36' 30" S, 90° 39' 57" W), and the following islets: Champion (1° 14' 7" S, 90° 23' 8" W); Gardner-by-Floreana ("Gardner") (1° 19' 52" S, 90° 17' 20" W); and Tortuga Islet (1° 1' 21.5" S, 90° 52' 11.5" W). Galapagos racers typically have a bi-modal pattern of peak activity occurring between approximately 05:30 h to 10:00 h and 16:00 h to 19:00 h (Altamirano, 1996; Christian, 2017). We searched for

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[1] Ecology and Conservation Lab, School of Natural and Computational Sciences, Massey University, Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand.
[2] Dirección de Ecosistemas, Dirección del Parque Nacional Galápagos, Av. Charles Darwin, S/N Puerto Ayora, Santa Cruz, Islas Galápagos, Ecuador.
[3] Fauna & Flora International, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, United Kingdom.
* Corresponding author. E-mail: l.ortiz-catedral@massey.ac.nz

racers during these peak activity periods and captured them by hand. Every captured racer was placed in a cloth bag, measured, weighed, photographed and faecal samples obtained. The total processing time per snake from capture to last measurement took approximately one hour.

We obtained faecal samples using a palpation technique. This method is minimally invasive and has been successfully used to yield useful dietary information in closely related snakes (Daltry et al., 1996; Williams et al., 2016). To extract faecal samples, individual Galapagos racers were held firmly in one hand around the mid-body. Gentle pressure was then applied slowly to palpate the intestinal tract, three quarters of the way down the body until faecal matter was extruded. Due to the delicate nature of this procedure, training in the field was provided by J. C. Daltry (see also Daltry et al. 1995; Williams et al., 2016). Faecal samples were collected in 2 ml micro-centrifuge tubes and fixed in 0.5-1.5 ml of 96 % ethanol until examination for contents. An alternative method to identify prey items is forced regurgitation (Drummond and Garcia, 1989; Manjarrez et al., 2013), but this method is more invasive and requires finding snakes in the process of ingesting or recently ingested prey, which only applied to 7 % of our encounters with racers on the Galapagos Islands.

Faecal samples were examined using dissection microscopes at the Invertebrate Collection Lab of the Charles Darwin Research Station in Puerto Ayora, Santa Cruz, Ecuador. We recorded the presence of scales, invertebrate remains, feathers, bones and other undigested materials. We also examined under the same microscopes reference voucher specimens of potential prey items from the vertebrate collection at the Charles Darwin Research Station (darwinfoundation.org/en/datazone). The prey remains in faecal samples were often large enough to be identified at the species level, but due to the fragmented nature of most of the material, we were unable to estimate prey size or age. Of the 79 faecal samples collected via the palpation technique, only 54 samples (from eight localities) had identifiable material (Table 1). The remaining 25 samples (from Champion and Gardner Islets) had material too digested to allow identification under a microscope. After examination, samples were returned to plastic tubes and deposited at the Directorate of the Galápagos National Park.

Table 1 summarises the variety of prey items identified in faecal samples of six species of Galapagos racers. The most frequently identified prey in our samples were lava lizards (*Microlophus* spp.) (28 samples), recorded in five of the six snake species. The second most common prey type identified from faecal samples were leaf-toed geckos (*Phyllodactylus* spp.), recorded from three snake species. The remains of small invertebrates (beetles, ants and centipedes) were also identified in 24 samples, but it is unclear if these represent secondary ingestion (e.g. invertebrates predated on by lizards). We also identified small feathers in 12 samples from a single species and population (*P. biserialis* on Gardner). Lastly, remains of avian eggshells were found in two samples from two populations. In addition to these samples, we observed eight predation events and one scavenging event. The predation events consisted of five instances of predation on hatchling marine iguanas (*A. cristatus*) on the coast of Cape Douglas (Fernandina Island), and one adult female lava lizard (*Microlophus albemarlensis*) by *P. occidentalis* at "La Cumbre", near the summit of Fernandina. The other two predation events were on lava lizards (*M. indefatigabilis*) on Seymour Norte by *Pseudalsophis dorsalis*. At Cape Douglas, Fernandina Island, we also observed the only instance of scavenging in this study: on the morning of July 5th 2018, we accidentally disturbed a large *P. occidentalis* in the process of ingesting a marine iguana hatchling. We captured the snake to obtain faecal samples and morphometric data. Two hours after, as we approached the site to release the snake, we observed a smaller racer ingesting the same partially digested marine iguana hatchling. We observed this snake ingest the whole hatchling and decided not to disturb the racer. Scavenging in the field has been documented for at least 43 snake species (DeVault and Krochmal, 2002). To the best of our knowledge, this is the first instance of scavenging reported for Galapagos racers.

Our study contributes to the knowledge on the basic biology of Galapagos racers and indicates that these terrestrial snakes are generalist predators across the archipelago, primarily ingesting reptiles (lava lizards and geckos). Our study also reports the first instances of birds and bird eggs as prey items for two racer species. Although the eggshells and feathers could not be identified to species level, we speculate these could belong to Darwin's finches (*Geospiza* spp., *Certhidea* spp. and/or *Camarhynchus* spp.), which are common on Gardner and Santa Fe where the faecal samples containing feather remains were collected. Regarding predation of avian prey, the closely related and similar-sized mainland species *Philodryas chamissonis* has been reported ingesting nestlings of two bird species (Greene and Kaksic, 1992; Escobar and Vukasovic, 2003; Torres, 2017). Combined with previous reports

Table 1. Prey identified in faecal samples of Galapagos racers (n = 54 including samples with no identifiable remains) at eight localities. Column numbers indicate the number of faecal samples containing prey per locality. a) *Microlophus grayii*; b) *M. indefatigabilis*; c) *M. albemarlensis*; d) *M. jacobi*; e) *M. duncanensis*; f) *Phyllodactylus baurii*; g) *P. galapagensis*; h) *P. duncanensis*.

Racer species	Locality	n	Lava lizard	Gecko	Invertebrate	Feather	Avian egg shell
Pseudalsophis biserialis	Champion	13	2^{a}	4^{f}	3		
	Gardner	41	11^{a}	6^{f}	14	12	
P. dorsalis	Santa Fe	4	2^{b}				1
P. occidentalis	Fernandina	7	3^{c}	2^{g}			
P. thomasi	Rabida	3	2^{d}				
	Santiago	3	2^{d}	3^{g}	1		
P. occidentalis	Tortuga	6	4^{c}	5^{g}	5		1
P. slevini	Pinzon	2	2^{e}	2^{h}	1		

of *P. biserialis* inspecting active nests of finches and mockingbirds (*Mimus* spp.) (Ortiz-Catedral, et al., 2017), this suggests that nestlings could be common prey for Galapagos racers, but this aspect, along with the potential consumption of avian eggs, requires further investigation.

No evidence of mammalian hair, teeth or claws were found in the faecal samples, but most samples were collected from racers on islands that lack terrestrial mammals. We cannot rule out the possibility that Galapagos racers would opportunistically prey on small native or non-native rodents. West Indian racers in the genus *Alsophis*, for example, show many morphological and ecologically similarities to the genus *Pseudalsophis* and, while most species feed primarily on lizards, other prey including birds, frogs, fishes and small rodents such as *Mus musculus* and juvenile *Rattus rattus* have also been reported (Henderson & Powell, 2009; Questel, 2012). We did not encounter seeds in our collection of faecal samples on eight islands, therefore cannot confirm whether *Pseudalsophis* spp. consumes fruit pulp on other islands.

Our study reports five previously undocumented prey species: *Microlophus grayii* and *Phyllodactylus baurii* for *P. biserialis* on Champion and Gardner Islets; *P.s. galapagensis* for *P. occidentalis* on Tortuga Islet; *M. duncanensis* for *P. slevini* on Pinzon Island; and *M. indefatigabilis* for *P. dorsalis* on Santa Fe and Seymour Norte Islands. Our study shows that the palpation technique can reliably yield material for field studies on the diet of Galapagos racers. We recommend examining whether Galapagos racers consume fruit pulp if presented with it in a captive setting, to verify whether these items represent a relevant component of their diet. We hope this study promotes further studies on the feeding ecology of Galapagos racers and their mainland relatives, to advance our knowledge of the niche breadth and potential dietary shifts associated with the colonisation of the Galapagos Islands. These studies will positively impact our ability to conserve, this diverse, yet neglected component of the Galapagos fauna.

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Diet of the Floreana mockingbird (*Mimus trifasciatus*) during the dry season on Champion and Gardner Islets, Galápagos Islands, Ecuador

CHARLES WITTMER-NARANJO
Universidad Tecnológica Internacional, Quito, Ecuador

ENZO M.R. REYES
Ecology and Conservation Lab, Institute of Natural and Mathematical Sciences, Massey University,
Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand

HÉCTOR ESTEBAN TERNEUS JÁCOME
Universidad Tecnológica Internacional, Quito, Ecuador

DANNY RUEDA
CHRISTIAN SEVILLA
Dirección de Ecosistemas, Dirección General del Parque Nacional Galápagos, Av. Charles Darwin, S/N
Puerto Ayora, Santa Cruz, Islas Galápagos, Ecuador

LUIS ORTIZ-CATEDRAL*
Ecology and Conservation Lab, Institute of Natural and Mathematical Sciences, Massey University,
Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand

Abstract: The Floreana mockingbird (*Mimus trifasciatus*) is one of the most endangered passerines in the world, with a global population of *c.* 400 individuals, restricted to two isolated islets: Champion and Gardner-by-Floreana. Due to its rarity and the inaccessibility to these islets, the biology of the Floreana mockingbird has remained poorly documented. Here we present a study on the diversity of food items consumed by Floreana mockingbirds prior to the rainy season. We recorded 269 foraging bouts, from 148 individuals on three independent sampling events. Floreana mockingbirds exhibited a generalist diet, which included flowers, nectar, stamens, sap, fruits, seeds, and seedlings from 12 plant species; larvae, pupae and adults of at least 10 arthropod orders; and small vertebrate prey, carrion, and egg contents. The diversity of food items between months and islets supports the idea of a generalist diet for the species. Our study provides useful information to identify and monitor the abundance of key resources for the species as part of the restoration of Floreana Island.

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Key words: bird behaviour, conservation, generalist diet, island avifauna, scavenging

INTRODUCTION

Developing management strategies for species of conservation interest requires an understanding of the biology of the target species. For instance, the successful conservation of the kakapo (*Strigops habroptilus*) (a nocturnal flightless parrot from New Zealand) has been fine-tuned since the 1970s as more research on the mating system and dietary requirements of the species is developed (Harper *et al.* 2006). Additionally, an understanding of the food preferences of a species can help managers identify

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*Correspondence: *l.ortiz-catedral@massey.ac.nz*

suitable areas for reintroduction (Kelle *et al.* 2014). Unfortunately, the biology of many endangered species remains poorly documented. One example is the Floreana mockingbird (*Mimus trifasciatus*), one of four species of mockingbirds endemic to the Galapagos Islands (Arbogast *et al.* 2006).

The mockingbirds (*Mimus* spp.) of the Galapagos Islands played an important role in the development of Darwin's theories about natural selection (Nicholls 2015); however, compared to Darwin's finches (*Geospiza, Camarhynchus, Certhidea,* and *Platyspiza* spp.) they have been the subject of fewer field studies. Four species of mockingbird exist in the Galapagos archipelago, all within the genus *Mimus* (Arbogast *et al.* 2006). Three of these are endemic to a single island, and their near-shore islets, all located in the south-east of the archipelago: the Española mockingbird (*M. macdonaldi*), the Floreana mockingbird (*M. trifasciatus*), and the San Cristobal mockingbird (*Mimus melanotis*). The fourth species, the Galapagos mockingbird (*M. parvulus*) occurs on nine main islands and several islets across the centre, north, and west of the archipelago (Arbogast *et al.* 2006; Hoeck *et al.* 2010a). A subspecies of Galapagos mockingbird (*M. parvulus bauri*) represents a lineage of hybrid ancestry between the San Cristobal mockingbird and Galapagos mockingbird (Nietlisbach *et al.* 2013) indicating temporary co-occurrence of two species on a single island. Lastly, the co-occurrence of two species of mockingbirds on a single island has been reported on Gardner-by-Floreana, where a single San Cristobal mockingbird coexisted in a population of Floreana mockingbirds for at least 10 months (Ortiz-Catedral *et al.* 2021).

The endangered Floreana mockingbird was historically present on the lowlands of Floreana Island, but became extinct on its namesake island due to the effects on introduced species and large-scale habitat modification by early inhabitants on Floreana Island (Curry 1986; Steadman 1986; Grant *et al.* 2000). Two remnant populations, geographically and genetically isolated on the islets of Champion and Gardner-by-Floreana, represent the last strongholds for the species (Hoeck *et al.* 2010b), with an estimated population of 400 individuals on both islets (Ortiz-Catedral 2018). In order to increase the geographic range and population size of the species, a reintroduction plan to the lowlands of Floreana has been developed (Charles Darwin Foundation 2008; Hoeck *et al.* 2010b), and a range of reintroduction scenarios had been analysed taking into account the genetics of the remnant populations (Bozzuto *et al.* 2017). However, to date there is only limited information on the range of food types and species that Floreana mockingbirds consume (Ortiz-Catedral 2014, 2018; Ortiz-Catedral *et al.* 2017). Prior to the reintroduction of the species to the lowlands of Floreana Island, it is imperative to determine whether their preferred prey items occur at potential release locations, and also how these resources increase in abundance as the restoration of Floreana Island progresses. Nevertheless, the diversity of food items that Floreana mockingbirds consume has not been quantified. We conducted a field study on the diversity of foods consumed by Floreana mockingbirds during the dry season, three months prior to the typical breeding season of the species: November, December (2015), and January (2016) (Ortiz-Catedral *et al.* 2017) in order to characterise the range of food species that need to be monitored on Floreana Island to assess whether their abundance can sustain a reintroduced population of Floreana mockingbirds in the near future.

METHODS

Our study was conducted on two islets: Champion (9.4 ha) (90°21′47″W, 01°13′55″S) and Gardner-by-Floreana (80 ha) (90°17′44″W, 01°20′48″S). Both islets represent land fragments of Floreana Island, which historically had a much larger area than present (Ali & Aitchinson 2014). Access to these islets is highly restricted and the Directorate of the Galapagos National Park have implemented stringent biosecurity measures in place to prevent the accidental introduction of invasive species. Further, both islets harbour remnant populations of vertebrate species now extinct on Floreana Island, including the Floreana mockingbird (Grant *et al.* 2000) and the Western Galapagos racer (*Pseudalsophis biserialis*) (Ortiz-Catedral *et al.* 2019), and are thus considered islets of high conservation value. Therefore, we visited the islets for two to a maximum of two to four days to conduct observations in November and December 2015 and January 2016. All biosecurity protocols were followed as part of this research. We conducted observations from 0600 h to 1800 h with a recess from 1200 h to 1400 h during the hottest period of the day, when mockingbirds are less active (Ortiz-Catedral *pers. obs.*). Individual observers (2–4) covered the study areas on foot: the total accessible land area of Champion, equivalent to 9 ha, and a 12 ha section of Gardner known as "The Plateau". The Plateau has been a study area for the population of Floreana mockingbirds for previous studies (see Ortiz-Catedral 2014; Hoeck *et al.* 2010b), and represents the only part of the islet that can be accessed safely. Whenever a mockingbird was encountered, the location, time, height to nearest 0.5 m, and only the first food item consumed within 30 seconds from sighting were noted to maximise independence of observations. Birds were observed at an approximate distance of 5 to 15 m using 8 x 42 binoculars.

Table 1. Plant and animal species consumed by Floreana mockingbirds on Champion and Gardner-by-Floreana (Gardner) from November 2015 to January 2016. ND indicates not determined.

Order/Family	Common name	Scientific name	Champion	Gardner	Part eaten
Boraginales/Boraginaceae	Muyuyo	*Cordia lutea*	0	1	Fruit
Boraginales/Boraginaceae	Heliotrope	*Heliotropium angiospermum*	0	1	Flower
Caryophyllales/Aizoaceae	Galapagos carpetweed	*Sesuvium edmonstonei*	2	0	Flower
Caryophyllales/Cactaceae	Prickly pear	*Opuntia megasperma*	51	14	Stamens, nectar, sap
Caryophyllales/ Nyctaginaceae	Wartclub	*Commicarpus tuberosus*	0	1	Seedling
Caryophyllales/Portulacaceae	Galapagos purslane	*Portulaca howellii*	0	13	Flower
Caryophyllales/Portulacaceae	Common purslane	*Portulaca oleracea*	1	0	Flower
Euphorbiales/Euphorbiaceae	Chala	*Croton scouleri*	1	3	Seed, seedling
Solanales/Convolvulaceae	Lava morning-glory	*Ipomoea habeliana*	5	0	Flower
Solanales/Solanaceae	Galapagos ground cherry	*Physalis galapagoensis*	13	2	Fruit
Solanales/Solanaceae	Galapagos shore petunia	*Exedeconus miersii*	0	4	Fruit, seeds
Lamiales/Verbenaceae	Galapagos lantana	*Lantana peduncularis*	0	1	Flower
Araneae/Araneidae	Garden orb-web spider	*Argiope trifasciata*	2	0	Adult
Araneae/Lycosidae	Wolf spider	*Hogna albemarlensis*	1	1	Adult
Blattodea/Kalotermitidae	Termite	*Incisitermes sp.*	1	2	Larvae
Diptera/Syrphidae	Fly	*Ornidia obesa*	0	3	Adult
Hymenoptera/Vespidae	Yellow paper wasp	*Polistes versicolor*	1	0	Adult
Neuroptera/Myrmeleontidae	Galapagos antlion	*Galapagoleon darwini*	0	1	Adult
Orthoptera/Acrididae	Large panted locust	*Schistocerca melanocera*	12	15	Adult
Scolopendromorpha/ Scolopendridae	Galapagos centipede	*Scolopendra galapagoensis*	1	0	Adult
Solifugae/Ammotrechidae	Sun spider	*Neocleobis solitarius*	0	1	Adult
Columbiformes/Columbidae	Galapagos dove	*Zenaida galapagoensis*	0	1	Egg contents
Pinnipedia/Otariidae	Galapagos sealion	*Zalophus wollebaeki*	10	0	Carrion
Squamata/Gekkonidae	Floreana gecko	*Phyllodactylus baurii*	0	1	Adult
Squamata/Tropiduridae	Floreana lava lizard	*Microlophus grayii*	1	1	Adult, carrion
Suliformes/Sulidae	Nazca booby	*Sula granti*	0	4	Egg contents
Araneae	Spider	ND	7	3	Adult
Lepidoptera	Moth, butterfly	ND	0	3	Adult, caterpillar, pupae
Blattodea	Cockroach	ND	1	1	Adult
Excoetidae	Flying fish	ND	0	1	Carrion
Coleoptera	Beetle	ND	1	4	Adult
Diptera	Fly	ND	11	6	Adult
Formicidae	Ant	ND	1	7	Adult
Gryllidae	Cricket	ND	0	7	Adult
ND	Arthopod	ND	17	29	Adult
-	Pebble	-	1	0	Non-dietary

Efforts were made to identify food items to species or at least major taxonomic groups (i.e. family or order for invertebrates). Plant food types were assigned to the following categories: flower bud, stamens, nectar, fruit, seeds, seedling, sap. Animal food types were classified as either invertebrate or vertebrate. Invertebrate food items were assigned to the following categories: larvae, pupae, adult. Vertebrate food items were classified as: carrion, egg contents, adult, or juvenile. Whenever possible we classified the foraging behaviour for each feeding bout according to the proposed terminology by Remsen & Robinson (1990). However, in over 30% of cases we could not clearly classify the type of foraging behaviour. Foraging behaviours are thus presented only for descriptive purposes. We analysed our data, as absolute frequency of occurrence (Wright 2010) per month, between populations, using Fisher's exact test in R (R Core Team 2020). We excluded the ingestion of sap (two observations) and pebbles from statistical analyses due to the low number of observations of these items. We also contrasted foraging heights per islet per sampling period using a two-sample t-test.

RESULTS

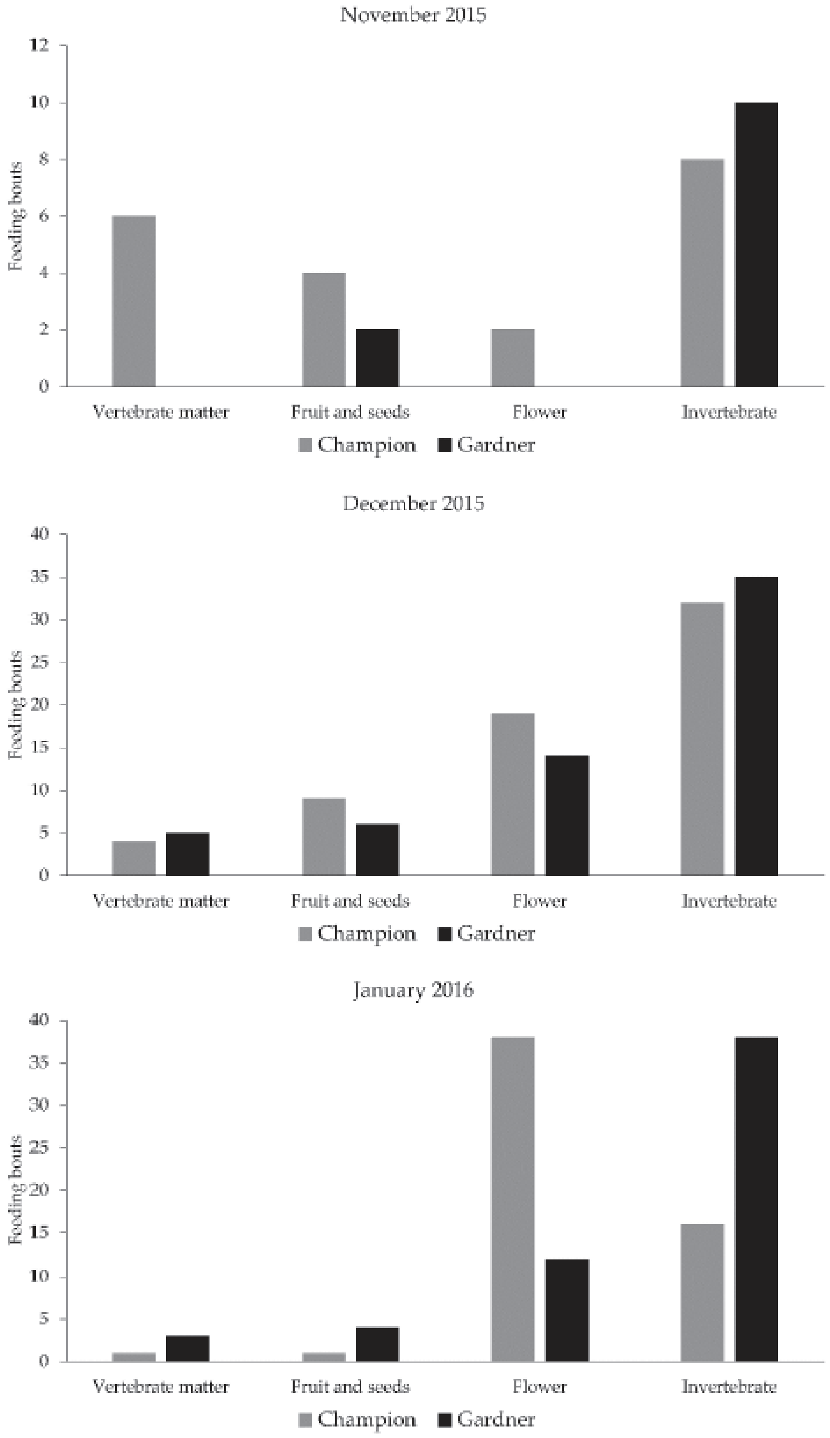
We recorded a total of 269 incidental foraging bouts by Floreana mockingbirds during November 2015 to January 2016 on 26 species of plants, invertebrates and vertebrates (Table 1). Floreana mockingbirds ingested invertebrate prey (larvae, pupae, adult insects), flowers (including petals, stamens, nectar, whole flowers), fruits, seeds, and seedlings, and vertebrate matter including carrion, small vertebrate prey, and contents of bird's egg. (Table 1). We also recorded a single instance of a non-dietary item ingestion, small pebbles (Table 1). In general, Floreana mockingbirds fed on similar food types in November and December (Fisher's exact test November P = 0.06, n = 32; Fisher's exact test December P = 0.71, n = 124). In January, Floreana mockingbirds on Champion fed predominantly on flowers, while on Gardner-by-Floreana, they consumed primarily invertebrates (Fisher's exact test January P < 0.001, n = 113) (Fig. 1). Floreana mockingbirds on Champion and Gardner-by-Floreana foraged on resources at the same height in November, but as our sampling progressed, individuals on Champion foraged at significantly higher strata than on Gardner-by-Floreana (Table 2). Floreana mockingbirds captured invertebrate prey using a variety of methods including: glean (flies, ants, spiders), flush pursue (Galapagos painted locust *Schistocerca melanocera*, yellow paper wasp *Polystes versicolor*), flake (termites), leap (Galapagos painted locust), lunge (Galapagos centipede *Scolopendra galapagoensis*, sun spider *Neocleobis solitarius*), and peck (termites). Floreana mockingbirds captured small vertebrates using lunge (Floreana lava lizard *Microlophus grayii*) and flake (Floreana gecko *Phyllodactylus baueri*). Floreana mockingbirds pulled pieces of carrion for ingestion, drank egg contents (Nazca booby *Sula granti*, Fig. 2; Galapagos dove *Zenaida galapagoensis*) and drank sap (prickly pear *Opuntia megasperma*). Fruits, and flowers were foraged by reach (Uvilla *Physalis peruviana*; purslane *Portulaca howellii*) and stamens and nectar by probe (prickly pear). With the exception of the yellow paper wasp, all species registered in our study are native species to the Galapagos Islands.

DISCUSSION

The diversity of food types and species consumed by Floreana mockingbirds during our study indicates that it is a generalist species, like the Galapagos mockingbird (*M. parvulus*) which feeds on a variety of invertebrates (Grant & Grant 1979; Curry 1986), booby (*Sula* spp.) blood (Curry & Anderson 1987), and even introduced mice (*Mus musculus*) (Gotanda *et al.* 2015). Similarly, another island species, the Socorro mockingbird (*Mimoides graysoni*) endemic to Socorro Island, Mexico consumes arthropods and fruits of at least seven plant species (Martinez-Gomez *et al.* 2001). Prior to our study, preliminary information on the breeding season diet of Floreana mockingbirds showed the consumption of nectar, pollen, and invertebrates (Ortiz-Catedral 2014). Our observations thus expand the list of known dietary items for the species. The consumption of carrion from sea lions (*Zalophus wollebaeki*), Floreana lava lizard (*Microlophus grayii*), and flying fish (Excoetidae) are of interest as these have not been documented for the species before. The

Table 2. Monthly changes in foraging height (m) of Floreana mockingbirds on Champion and Gardner Islets. *Significant differences.

Month	n	Champion	Gardner	t value	*P*
November	33	0.10 ± 0.34	0	1.28	0.21
December	125	0.37 ± 0.81	0.11 ± 0.39	2.25	0.03*
January	106	1.06 ± 0.92	0.27 ± 0.56	5.32	<0.001*


November 2015

December 2015

January 2016

Figure 1. Monthly changes in proportion of food types in Floreana mockingbirds on Champion and Gardner-by-Floreana ("Gardner").

Figure 2. Floreana mockingbird (*Mimus trifasciatus*) drinking the contents of a Nazca booby (*Sula granti*) egg on Gardner-by-Floreana. Photograph: L. Ortiz-Catedral.

drinking of egg contents of Nazca boobies (*Sula granti*) and Galapagos dove (*Zenaida galapagoensis*) also represent new records on the diversity of foods consumed by the species, a trait shared with Española mockingbirds (Hatch 1965; Harris 1968). Harris (1968) suspected Floreana mockingbirds fed on eggs and nestlings of blue-footed boobies (*Sula nebouxii*), based on the disappearance of an egg and hatchling in a single nest on Gardner-by-Floreana, but did not directly observe mockingbirds. In fact, based on the description provided, we suspect that the predation of an egg and hatchling of blue-footed booby described in Harris (1968) more likely represents scavenging by Western Galapagos racers (*Pseudalsophis biserialis*), an endemic terrestrial snake (see Ortiz-Catedral *et al.* 2017; Ortiz-Catedral *et al.* 2019). Similarly, Bowman & Carter (1971) suspected that the ingestion of bird eggs was a trait shared by all mockingbird species in the Galapagos islands. They observed Floreana mockingbirds pecking at blue-footed booby (*Sula nebouxii*) eggs without breaking them, and in controlled experiments they induced starvation on Floreana mockingbirds and offered them broken chicken eggs, which the mockingbirds consumed (Bowman & Carter 1971). Therefore, our observations of consumption of egg contents of Nazca booby (Fig. 2) and Galapagos dove represent the first confirmed record in the wild of ingestion of this resource by Floreana mockingbirds.

The Galapagos Islands have suffered large-scale habitat modification prompted by the settlement of humans on the islands in the last 200 or so years (Watson *et al.* 2009), and the introduction of invasive species (Mauchamp 1997; Wikelski *et al.* 2004; Tye 2006; Wiedenfeld *et al.* 2007). This in turn has been associated with reductions in population size, and local extinction of vertebrate species on human inhabited islands, like Floreana Island (Grant *et al.* 2005; Dvorak *et al.* 2017). Nevertheless, since the late 1960s there have been numerous efforts to control or eradicate introduced species from various islands across the archipelago (Cruz *et al.* 2009; Carrion *et al.* 2011), in an effort to restore populations of endemic species (Donlan *et al.* 2007) and more recently, to holistically restore island ecosystems and species' function via reintroductions of locally extinct taxa, such as the Floreana tortoise (*Chelonoidis nigra*) (Hunter *et al.* 2019). The Floreana mockingbird is one of the bird species identified for reintroduction to the lowlands of Floreana Island in coming years (Charles Darwin Foundation 2008; Hoeck *et al.* 2010b; Bozzuto *et al.* 2017).

At this stage however, there is uncertainty about how long after the eradication of introduced species, the lowlands of Floreana will be suitable for reintroducing Floreana mockingbirds. Examples on other systems show that habitat enhancement, for instance via supplementary feeding and targeted restoration of food resources can assist in the reintroduction of critically endangered species (Maggs *et al.* 2019). Our study provides information on the diversity and temporal changes in diet composition of the remnant populations of this endangered species prior to the wet season, and can therefore be used to identify species to monitor on Floreana Island as groundwork for the eventual reintroduction of this endemic species to its namesake island. Future studies should aim to characterise the diet of the species immediately after the breeding season and explore the relationships between group size and territory quality.

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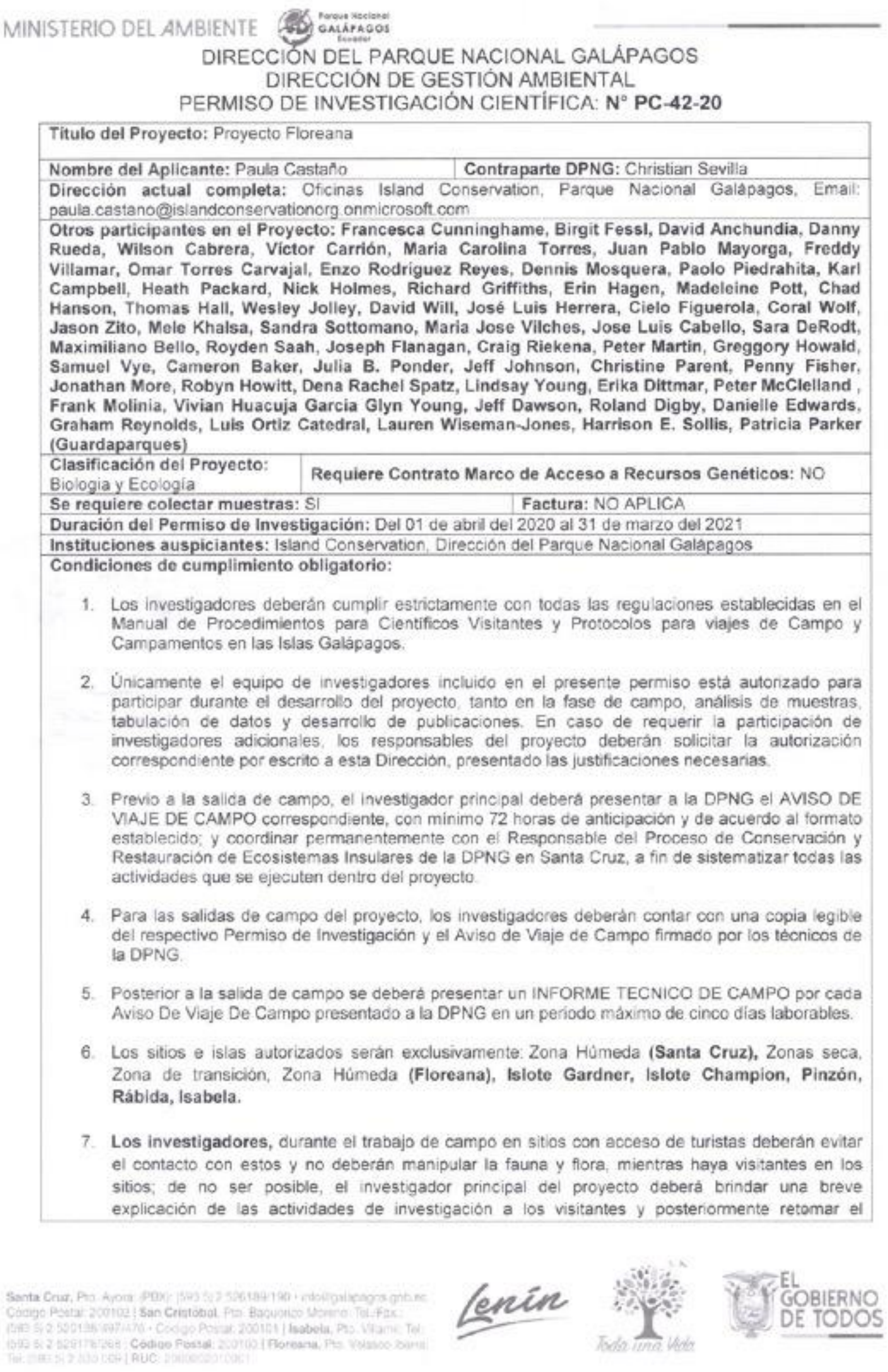
7.5 APPENDIX 5

Galápagos research permit in Spanish



MINISTERIO DEL AMBIENTE

Parque Nacional Galápagos Ecuador

DIRECCIÓN DEL PARQUE NACIONAL GALÁPAGOS
DIRECCIÓN DE GESTIÓN AMBIENTAL
PERMISO DE INVESTIGACIÓN CIENTÍFICA: **N° PC-42-20**

Título del Proyecto: Proyecto Floreana

Nombre del Aplicante: Paula Castaño

Contraparte DPNG: Christian Sevilla

Dirección actual completa: Oficinas Island Conservation, Parque Nacional Galápagos, Email: paula.castano@islandconservationorg.onmicrosoft.com

Otros participantes en el Proyecto: Francesca Cunninghame, Birgit Fessl, David Anchundia, Danny Rueda, Wilson Cabrera, Víctor Carrión, Maria Carolina Torres, Juan Pablo Mayorga, Freddy Villamar, Omar Torres Carvajal, Enzo Rodríguez Reyes, Dennis Mosquera, Paolo Piedrahita, Karl Campbell, Heath Packard, Nick Holmes, Richard Griffiths, Erin Hagen, Madeleine Pott, Chad Hanson, Thomas Hall, Wesley Jolley, David Will, José Luis Herrera, Cielo Figuerola, Coral Wolf, Jason Zito, Mele Khalsa, Sandra Sottomano, Maria Jose Vilches, Jose Luis Cabello, Sara DeRodt, Maximiliano Bello, Royden Saah, Joseph Flanagan, Craig Riekena, Peter Martin, Greggory Howald, Samuel Vye, Cameron Baker, Julia B. Ponder, Jeff Johnson, Christine Parent, Penny Fisher, Jonathan More, Robyn Howitt, Dena Rachel Spatz, Lindsay Young, Erika Dittmar, Peter McClelland , Frank Molinia, Vivian Huacuja Garcia Glyn Young, Jeff Dawson, Roland Digby, Danielle Edwards, Graham Reynolds, Luis Ortiz Catedral, Lauren Wiseman-Jones, Harrison E. Sollis, Patricia Parker (Guardaparques)

Clasificación del Proyecto: Biologia y Ecología

Requiere Contrato Marco de Acceso a Recursos Genéticos: NO

Se requiere colectar muestras: SI

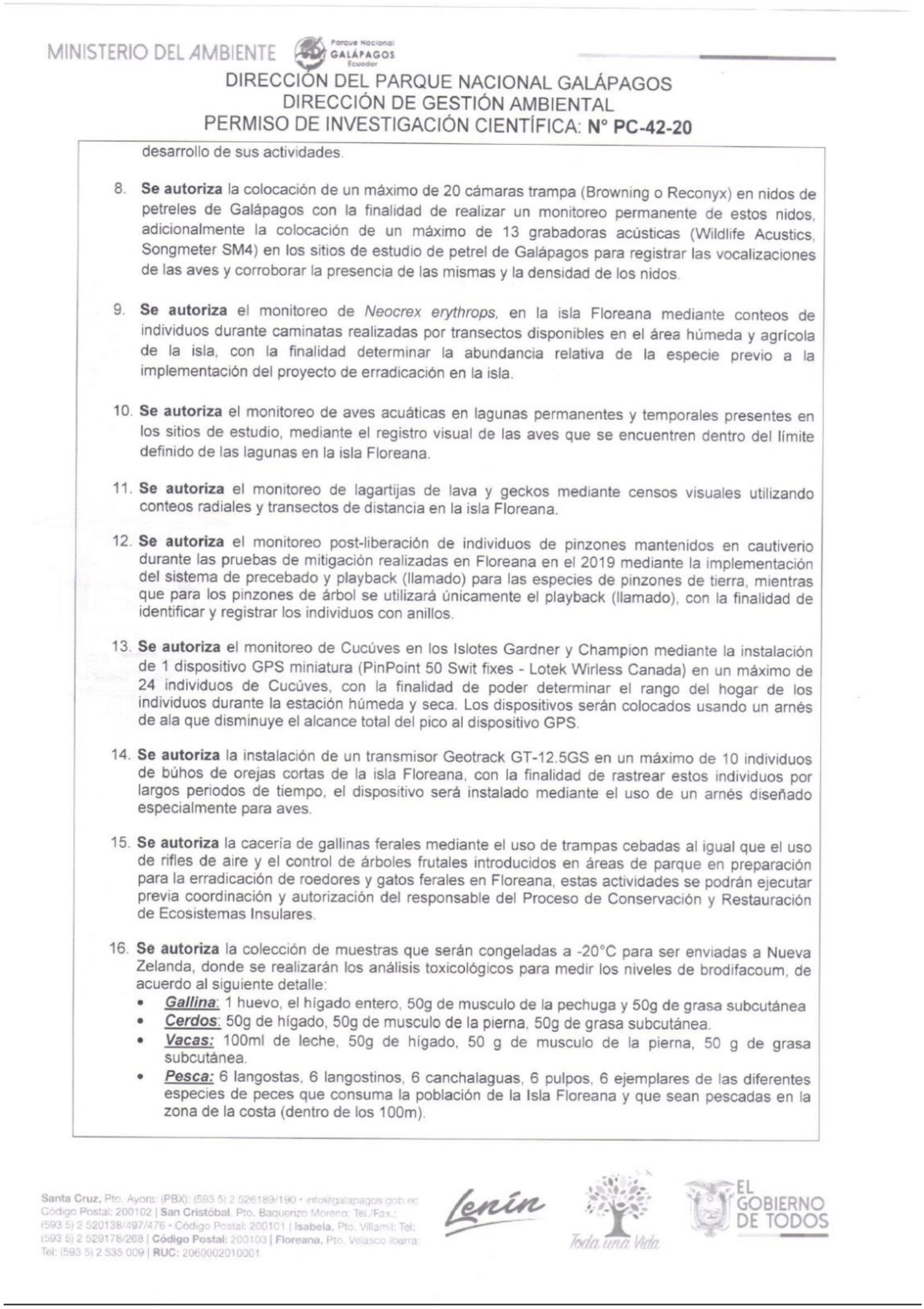
Factura: NO APLICA

Duración del Permiso de Investigación: Del 01 de abril del 2020 al 31 de marzo del 2021

Instituciones auspiciantes: Island Conservation, Dirección del Parque Nacional Galápagos

Condiciones de cumplimiento obligatorio:

1. Los investigadores deberán cumplir estrictamente con todas las regulaciones establecidas en el Manual de Procedimientos para Científicos Visitantes y Protocolos para viajes de Campo y Campamentos en las Islas Galápagos.
2. Únicamente el equipo de investigadores incluido en el presente permiso está autorizado para participar durante el desarrollo del proyecto, tanto en la fase de campo, análisis de muestras, tabulación de datos y desarrollo de publicaciones. En caso de requerir la participación de investigadores adicionales, los responsables del proyecto deberán solicitar la autorización correspondiente por escrito a esta Dirección, presentado las justificaciones necesarias.
3. Previo a la salida de campo, el investigador principal deberá presentar a la DPNG el AVISO DE VIAJE DE CAMPO correspondiente, con mínimo 72 horas de anticipación y de acuerdo al formato establecido; y coordinar permanentemente con el Responsable del Proceso de Conservación y Restauración de Ecosistemas Insulares de la DPNG en Santa Cruz, a fin de sistematizar todas las actividades que se ejecuten dentro del proyecto.
4. Para las salidas de campo del proyecto, los investigadores deberán contar con una copia legible del respectivo Permiso de Investigación y el Aviso de Viaje de Campo firmado por los técnicos de la DPNG.
5. Posterior a la salida de campo se deberá presentar un INFORME TECNICO DE CAMPO por cada Aviso De Viaje De Campo presentado a la DPNG en un periodo máximo de cinco días laborables.
6. Los sitios e islas autorizados serán exclusivamente: Zona Húmeda **(Santa Cruz),** Zonas seca, Zona de transición, Zona Húmeda **(Floreana), Islote Gardner, Islote Champion, Pinzón, Rábida, Isabela.**
7. **Los investigadores,** durante el trabajo de campo en sitios con acceso de turistas deberán evitar el contacto con estos y no deberán manipular la fauna y flora, mientras haya visitantes en los sitios; de no ser posible, el investigador principal del proyecto deberá brindar una breve explicación de las actividades de investigación a los visitantes y posteriormente retomar el



desarrollo de sus actividades.

8. **Se autoriza** la colocación de un máximo de 20 cámaras trampa (Browning o Reconyx) en nidos de petreles de Galápagos con la finalidad de realizar un monitoreo permanente de estos nidos, adicionalmente la colocación de un máximo de 13 grabadoras acústicas (Wildlife Acustics, Songmeter SM4) en los sitios de estudio de petrel de Galápagos para registrar las vocalizaciones de las aves y corroborar la presencia de las mismas y la densidad de los nidos.

9. **Se autoriza** el monitoreo de *Neocrex erythrops*, en la isla Floreana mediante conteos de individuos durante caminatas realizadas por transectos disponibles en el área húmeda y agrícola de la isla, con la finalidad determinar la abundancia relativa de la especie previo a la implementación del proyecto de erradicación en la isla.

10. **Se autoriza** el monitoreo de aves acuáticas en lagunas permanentes y temporales presentes en los sitios de estudio, mediante el registro visual de las aves que se encuentren dentro del límite definido de las lagunas en la isla Floreana.

11. **Se autoriza** el monitoreo de lagartijas de lava y geckos mediante censos visuales utilizando conteos radiales y transectos de distancia en la isla Floreana.

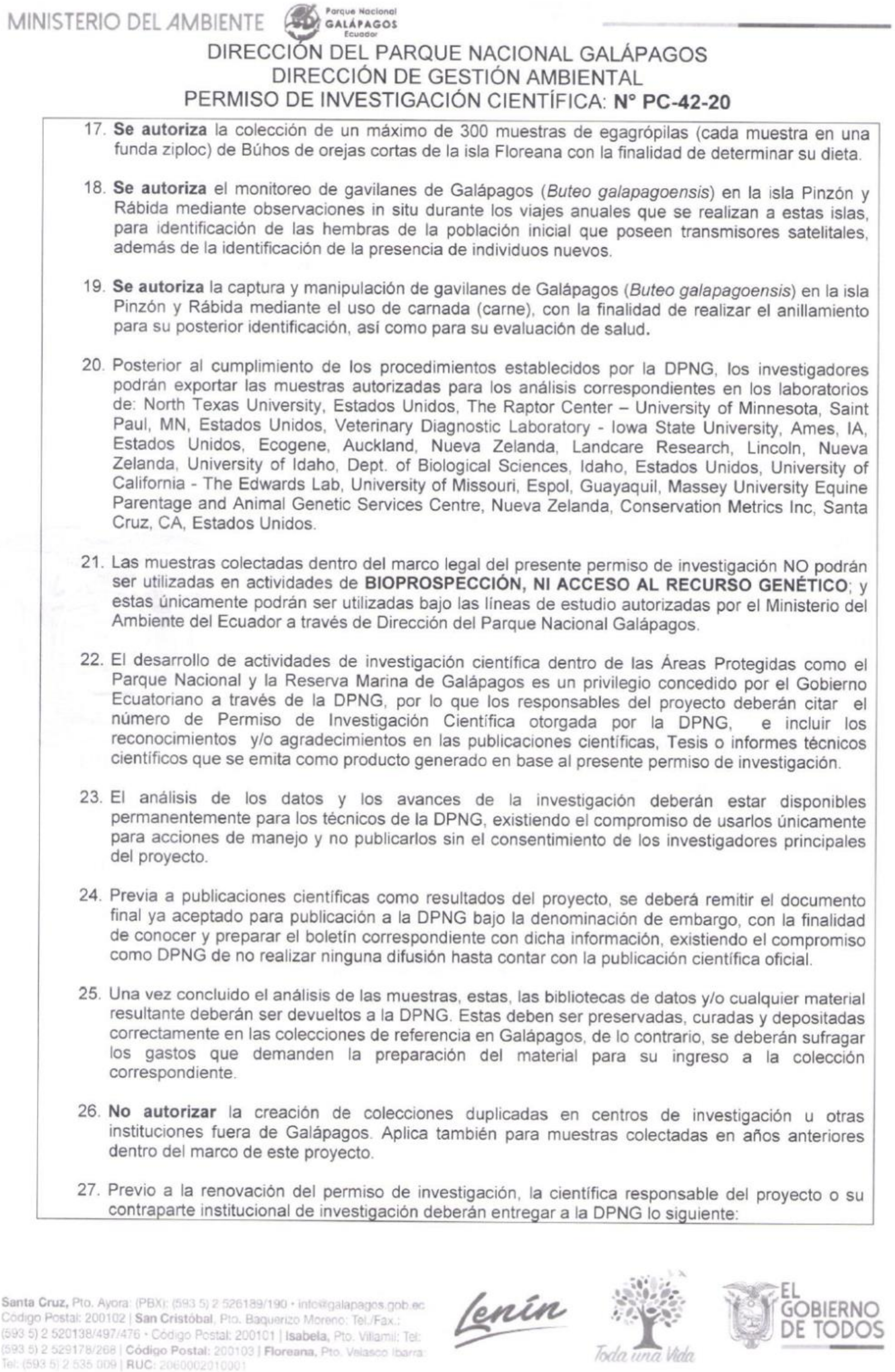
12. **Se autoriza** el monitoreo post-liberación de individuos de pinzones mantenidos en cautiverio durante las pruebas de mitigación realizadas en Floreana en el 2019 mediante la implementación del sistema de precebado y playback (llamado) para las especies de pinzones de tierra, mientras que para los pinzones de árbol se utilizará únicamente el playback (llamado), con la finalidad de identificar y registrar los individuos con anillos.

13. **Se autoriza** el monitoreo de Cucúves en los Islotes Gardner y Champion mediante la instalación de 1 dispositivo GPS miniatura (PinPoint 50 Swit fixes - Lotek Wirless Canada) en un máximo de 24 individuos de Cucúves, con la finalidad de poder determinar el rango del hogar de los individuos durante la estación húmeda y seca. Los dispositivos serán colocados usando un arnés de ala que disminuye el alcance total del pico al dispositivo GPS.

14. **Se autoriza** la instalación de un transmisor Geotrack GT-12.5GS en un máximo de 10 individuos de búhos de orejas cortas de la isla Floreana, con la finalidad de rastrear estos individuos por largos periodos de tiempo, el dispositivo será instalado mediante el uso de un arnés diseñado especialmente para aves.

15. **Se autoriza** la cacería de gallinas ferales mediante el uso de trampas cebadas al igual que el uso de rifles de aire y el control de árboles frutales introducidos en áreas de parque en preparación para la erradicación de roedores y gatos ferales en Floreana, estas actividades se podrán ejecutar previa coordinación y autorización del responsable del Proceso de Conservación y Restauración de Ecosistemas Insulares.

16. **Se autoriza** la colección de muestras que serán congeladas a -20°C para ser enviadas a Nueva Zelanda, donde se realizarán los análisis toxicológicos para medir los niveles de brodifacoum, de acuerdo al siguiente detalle:
    - ***<u>Gallina</u>:*** 1 huevo, el hígado entero, 50g de musculo de la pechuga y 50g de grasa subcutánea
    - ***Cerdos:*** 50g de hígado, 50g de musculo de la pierna, 50g de grasa subcutánea.
    - ***Vacas:*** 100ml de leche, 50g de hígado, 50 g de musculo de la pierna, 50 g de grasa subcutánea.
    - ***Pesca:*** 6 langostas, 6 langostinos, 6 canchalaguas, 6 pulpos, 6 ejemplares de las diferentes especies de peces que consuma la población de la Isla Floreana y que sean pescadas en la zona de la costa (dentro de los 100m).



17. **Se autoriza** la colección de un máximo de 300 muestras de egagrópilas (cada muestra en una funda ziploc) de Búhos de orejas cortas de la isla Floreana con la finalidad de determinar su dieta.

18. **Se autoriza** el monitoreo de gavilanes de Galápagos (*Buteo galapagoensis*) en la isla Pinzón y Rábida mediante observaciones in situ durante los viajes anuales que se realizan a estas islas, para identificación de las hembras de la población inicial que poseen transmisores satelitales, además de la identificación de la presencia de individuos nuevos.

19. **Se autoriza** la captura y manipulación de gavilanes de Galápagos (*Buteo galapagoensis*) en la isla Pinzón y Rábida mediante el uso de carnada (carne), con la finalidad de realizar el anillamiento para su posterior identificación, así como para su evaluación de salud.

20. Posterior al cumplimiento de los procedimientos establecidos por la DPNG, los investigadores podrán exportar las muestras autorizadas para los análisis correspondientes en los laboratorios de: North Texas University, Estados Unidos, The Raptor Center – University of Minnesota, Saint Paul, MN, Estados Unidos, Veterinary Diagnostic Laboratory - Iowa State University, Ames, IA, Estados Unidos, Ecogene, Auckland, Nueva Zelanda, Landcare Research, Lincoln, Nueva Zelanda, University of Idaho, Dept. of Biological Sciences, Idaho, Estados Unidos, University of California - The Edwards Lab, University of Missouri, Espol, Guayaquil, Massey University Equine Parentage and Animal Genetic Services Centre, Nueva Zelanda, Conservation Metrics Inc, Santa Cruz, CA, Estados Unidos.

21. Las muestras colectadas dentro del marco legal del presente permiso de investigación NO podrán ser utilizadas en actividades de **BIOPROSPECCIÓN, NI ACCESO AL RECURSO GENÉTICO**; y estas únicamente podrán ser utilizadas bajo las líneas de estudio autorizadas por el Ministerio del Ambiente del Ecuador a través de Dirección del Parque Nacional Galápagos.

22. El desarrollo de actividades de investigación científica dentro de las Áreas Protegidas como el Parque Nacional y la Reserva Marina de Galápagos es un privilegio concedido por el Gobierno Ecuatoriano a través de la DPNG, por lo que los responsables del proyecto deberán citar el número de Permiso de Investigación Científica otorgada por la DPNG, e incluir los reconocimientos y/o agradecimientos en las publicaciones científicas, Tesis o informes técnicos científicos que se emita como producto generado en base al presente permiso de investigación.

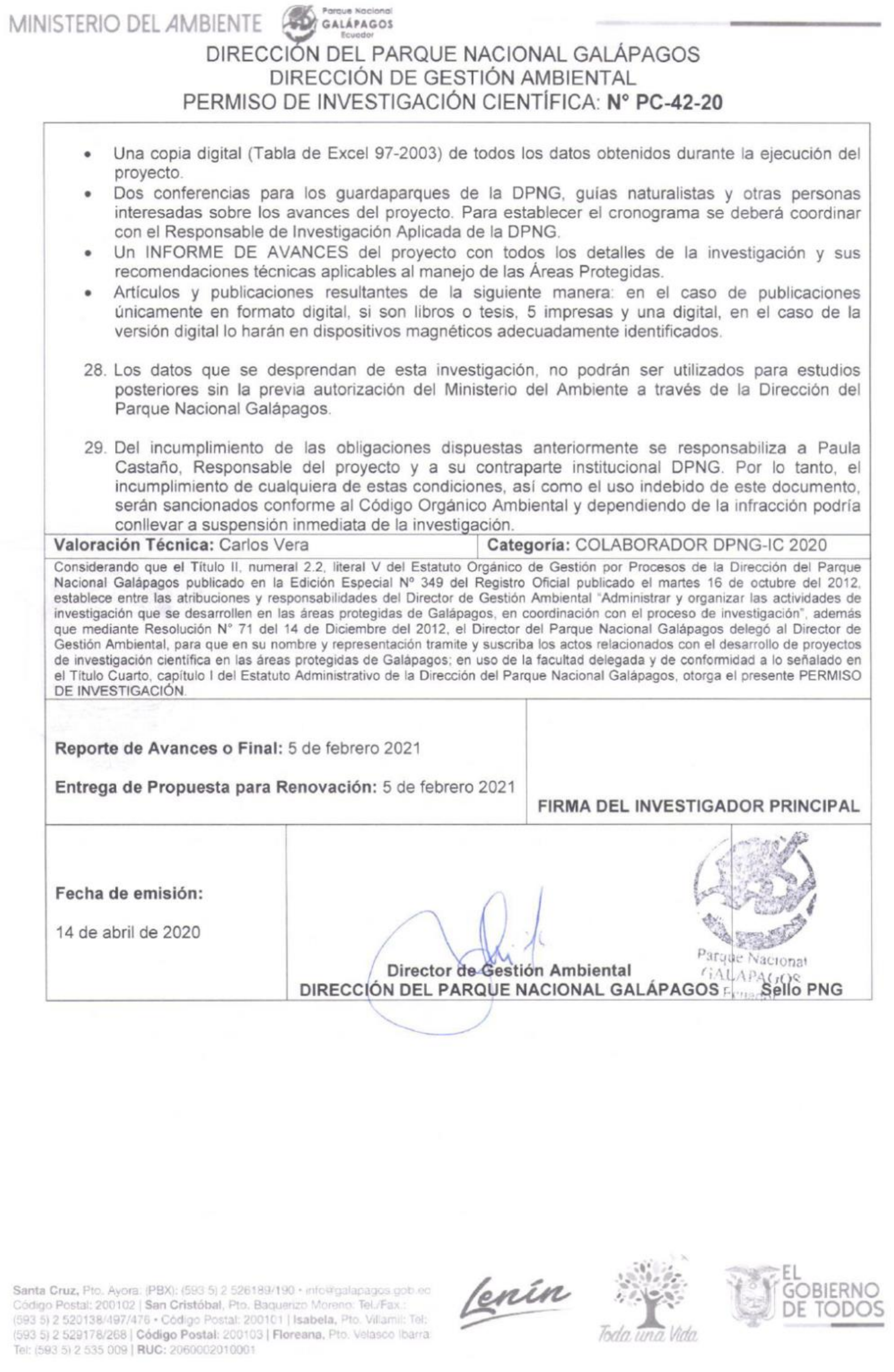
23. El análisis de los datos y los avances de la investigación deberán estar disponibles permanentemente para los técnicos de la DPNG, existiendo el compromiso de usarlos únicamente para acciones de manejo y no publicarlos sin el consentimiento de los investigadores principales del proyecto.

24. Previa a publicaciones científicas como resultados del proyecto, se deberá remitir el documento final ya aceptado para publicación a la DPNG bajo la denominación de embargo, con la finalidad de conocer y preparar el boletín correspondiente con dicha información, existiendo el compromiso como DPNG de no realizar ninguna difusión hasta contar con la publicación científica oficial.

25. Una vez concluido el análisis de las muestras, estas, las bibliotecas de datos y/o cualquier material resultante deberán ser devueltos a la DPNG. Estas deben ser preservadas, curadas y depositadas correctamente en las colecciones de referencia en Galápagos, de lo contrario, se deberán sufragar los gastos que demanden la preparación del material para su ingreso a la colección correspondiente.

26. **No autorizar** la creación de colecciones duplicadas en centros de investigación u otras instituciones fuera de Galápagos. Aplica también para muestras colectadas en años anteriores dentro del marco de este proyecto.

27. Previo a la renovación del permiso de investigación, la científica responsable del proyecto o su contraparte institucional de investigación deberán entregar a la DPNG lo siguiente:



MINISTERIO DEL AMBIENTE Parque Nacional GALÁPAGOS Ecuador

DIRECCIÓN DEL PARQUE NACIONAL GALÁPAGOS
DIRECCIÓN DE GESTIÓN AMBIENTAL
PERMISO DE INVESTIGACIÓN CIENTÍFICA: **N° PC-42-20**

- Una copia digital (Tabla de Excel 97-2003) de todos los datos obtenidos durante la ejecución del proyecto.
- Dos conferencias para los guardaparques de la DPNG, guías naturalistas y otras personas interesadas sobre los avances del proyecto. Para establecer el cronograma se deberá coordinar con el Responsable de Investigación Aplicada de la DPNG.
- Un INFORME DE AVANCES del proyecto con todos los detalles de la investigación y sus recomendaciones técnicas aplicables al manejo de las Áreas Protegidas.
- Artículos y publicaciones resultantes de la siguiente manera: en el caso de publicaciones únicamente en formato digital, si son libros o tesis, 5 impresas y una digital, en el caso de la versión digital lo harán en dispositivos magnéticos adecuadamente identificados.

28. Los datos que se desprendan de esta investigación, no podrán ser utilizados para estudios posteriores sin la previa autorización del Ministerio del Ambiente a través de la Dirección del Parque Nacional Galápagos.

29. Del incumplimiento de las obligaciones dispuestas anteriormente se responsabiliza a Paula Castaño, Responsable del proyecto y a su contraparte institucional DPNG. Por lo tanto, el incumplimiento de cualquiera de estas condiciones, así como el uso indebido de este documento, serán sancionados conforme al Código Orgánico Ambiental y dependiendo de la infracción podría conllevar a suspensión inmediata de la investigación.

Valoración Técnica: Carlos Vera	**Categoría:** COLABORADOR DPNG-IC 2020

Considerando que el Título II, numeral 2.2, literal V del Estatuto Orgánico de Gestión por Procesos de la Dirección del Parque Nacional Galápagos publicado en la Edición Especial N° 349 del Registro Oficial publicado el martes 16 de octubre del 2012, establece entre las atribuciones y responsabilidades del Director de Gestión Ambiental "Administrar y organizar las actividades de investigación que se desarrollen en las áreas protegidas de Galápagos, en coordinación con el proceso de investigación", además que mediante Resolución N° 71 del 14 de Diciembre del 2012, el Director del Parque Nacional Galápagos delegó al Director de Gestión Ambiental, para que en su nombre y representación tramite y suscriba los actos relacionados con el desarrollo de proyectos de investigación científica en las áreas protegidas de Galápagos; en uso de la facultad delegada y de conformidad a lo señalado en el Título Cuarto, capítulo I del Estatuto Administrativo de la Dirección del Parque Nacional Galápagos, otorga el presente PERMISO DE INVESTIGACIÓN.

Reporte de Avances o Final: 5 de febrero 2021 **Entrega de Propuesta para Renovación:** 5 de febrero 2021	**FIRMA DEL INVESTIGADOR PRINCIPAL**

Fecha de emisión: 14 de abril de 2020	**Director de Gestión Ambiental** **DIRECCIÓN DEL PARQUE NACIONAL GALÁPAGOS**	**Sello PNG**

Santa Cruz, Pto. Ayora: (PBX): (593 5) 2 526189/190 • info@galapagos.gob.ec Código Postal: 200102 | **San Cristóbal,** Pto. Baquerizo Moreno: Tel./Fax.: (593 5) 2 520138/497/476 • Código Postal: 200101 | **Isabela,** Pto. Villamil: Tel: (593 5) 2 529178/268 | **Código Postal:** 200103 | **Floreana,** Pto. Velasco Ibarra Tel: (593 5) 2 535 009 | **RUC:** 2060002010001

Lenín Toda una Vida EL GOBIERNO DE TODOS