Conserving Wilkins' Bunting (*Nesospiza wilkinsi*): an endangered, single island endemic

Heinz E. Ortmann

Supervisor: Dr Peter G. Ryan

February 2013, revised May 2013

Submitted in fulfillment of the requirements for the degree of Master of Science in Conservation Biology

---

Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa

heortmann@gmail.com

Table of Contents

PLAGIARISM DECLARATION

1. I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is ones own.

2. I have used the Conservation Biology Journal format as the convention for citation and referencing. Each significant contribution to, and quotation in, this project from the work, or works of other people has been attributed and has cited and referenced.

3. This project "Conserving Wilkins' Bunting (*Nesospzia wilkinsi*) - an endangered, island endemic" is my own work.

4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.
5. I acknowledge that copying someone else's assignment or essay, or part of it, is wrong, and declare that this is my own work

SIGNATURE: ________________________

DATE: ________________

Acknowledgements

This study would not have been possible without the support and input of a number of people, institutions and organisations providing the necessary funding, support, guidance and encouragement. I am grateful for the assistance of Dom Rollinson and Otto Whitehead during the initial phase of the field work. Without their assistance, especially Dom who shared his extensive knowledge on catching and ringing birds it would not have been possible to catch as many Wilkins' Buntings as we did. The RSPB project on the impacts of the *MS Oliva* oil spill on the Northern Rockhopper Penguins that occur on the Tristan archipelago provided the opportunity for this study to take place.

My supervisor, Peter Ryan, assisted me greatly, especially in improving my inadequacies when it comes to writing in a scientific manner as well as providing me with the opportunity of visiting the amazing island of Nightingale. Mention also needs to be made of all the equipment that he provided me with, without which this study would have never taken place.

A special mention must be made for Dieter Oschadleus who, at short notice, taught me as much as he could with regards to the intricacies of bird ringing. Within a few short weeks I was able to carry out all the essential skills that would be necessary on Nightingale Island.

Thank you to the Agricultural Research Council, for identifying the invasive scale insect for me, and in particular to Vivienne Uys who sorted out the whole process for me. Thanks also to Hilary Buchanan, Tania Jansen and Anthea Links of the Fitz who helped with the payment and getting the samples to the ARC.

To the field assistants from the Tristan Conservation Department, and Richard Cuthbert from RSPB, a big thank you for all the help in the field and coordinating the logistics of this project, respectively Julian Repetto, George Swain, Kirsty Green, Trevor Glass and Katrine Herian deserve special mention for their assistance whilst on Nightingale Island, helping out with showing us around and sharing some fantastic stories about Tristan Island. To my travel buddy of over 3 months, Antje Steinfurth, thank you for all the advice and doing most of the pre-travel preparation and buying of essential equipment that I had no idea that we needed.

I am indebted to the crew and all the people, of which there are too many to mention here, that made the trip to Tristan on the *SA Agulhas II* a success. I am especially thankful to the team from Starlite aviation that did an exceptional job in dropping us and all of our cargo off safely on Nightingale Island. A special mention must be made to Dudley, the pilot, whose skilled flying got us safely onto the island. Again mention must be made of the Tristan Conservation Department and all who helped with the big job of getting us, and all our equipment safely back to Tristan from Nightingale Island. For the time on Tristan it was a pleasure staying with Nicky and Emma Swain. The exemplary conduct and assistance of the crew aboard the *MV Edinburgh* and the friendly atmosphere on board made the trip home an absolute treat. Special mention needs to be made to the captain Clarence for making us feel welcome.

Financial support was provided by a number of different sources: RSPB, UCT and the Percy FitzPatrick Institute deserve special mention, as I was in no financial position to go on this trip without significant financial assistance. I was on a Rotary bursary for the coursework component of this Masters that made it possible for me to study this course, and pursue my interest in conservation. Finally I thank my family and friends for their support and encouragement, particularly during the write up phase of this study. To my CB classmates, noteworthy mentions for Kat Forsythe, Craig Harding and Caz Sanguinetti, thanks for the assistance and for sharing a few laughs even during the most stressful times.

Abstract

The conservation of oceanic island species, in particular single island endemics, is a vital facet of the field of conservation biology. Most bird extinctions that have occurred, in the last 500 years, have been of island endemics, and many other island endemics currently are faced with the threat of extinction. Wilkins' Bunting (*Nesospiza wilkinsi*) is one such species that is little known and occurs only on the remote South Atlantic Ocean Island of Nightingale. It is a presumed specialist feeder, reliant largely on the fruit of the localised Island Tree (*Phylica arborea*). The main aims of this study were to reassess Wilkins' Buntings' population size and determine territory sizes and densities of breeding pairs in the study area. This work focussed on catching and colour banding as many Wilkins' Buntings as possible during the field season on Nightingale Island from14 September to 26 November 2012, and recording observations of colour banded birds with a GPS to later analyse in ArcGIS for territory size. Gathering as much information as possible on the breeding biology of both Wilkins' and Nightingale buntings was the second major objective of this study. Another objective, not directly dealing with the buntings, was to provide baseline data that would help to determine the species' ability to withstand threats such as the possible reduction of fruit loads by an introduced greedy scale *Hemiberlesia rapax* (Comstock). The fruit loads on 10 terminal branchlets of up to 20 large trees within Wilkins' Bunting territories were counted to determine if any local variation existed across the island. By recording the presence and absence of the scale insect I managed to provide a current distribution and relative abundance for the species over a large area of the island. Four 50 m transects were also carried out in four different areas of the island to determine which size classes of *Phylica* trees are most affected by greedy scale, and to determine whether the scale insect was indeed lowering fruit loads as has been observed for another species of introduced scale *Coccus hesperidum* near Blenden Hall on Inaccessible Island. Territory sizes were small, 0.012ha - 0.34 ha. A positive result was that the number of pairs encountered was higher than previous estimates, with 56 pairs having a banded bird and approximately 80 pairs occurring on the island. Ten nests were found, eight containing eggs. Clutch size was 1-2 eggs and their breeding behaviour is similar to Inaccessible Buntings, except for the nests typically being built higher above the ground. Fruit loads do not seem to show significant local variation and although widespread, the scale insect appears to have

little impact on fruit loads across the island. However, the fact that all trees of less than 20 cm basal circumference sampled in transects had some level of scale insect infestation, is a cause for concern. There is plenty of scope for further research, especially focussing on breeding biology and survival rates of all age classes of buntings. Further work to determine the impacts of the scale insects are also recommended, as the introduction of the scale insect highlights the importance of also preventing further introductions. The work done here affirms the status of Endangered for Wilkins' Bunting as the population remains small (ca 250) and the threats to its persistence remain.

Chapter 1. General introduction and current knowledge of *Nesospiza* buntings, focussing on Wilkins' Bunting

Conservation of oceanic island species

Conservation on islands needs to be site specific and focussed on particular species, due to the uniqueness of each island, the larger proportion of threatened endemic species on islands (Biber 2002), and the higher rates and risk of extinction islands experience in comparison to mainland regions (Diamond 1984a, Reid & Miller 1989, Case et al. 1992). Evolutionary trends that favour specialisation, such as the loss of flight in birds (Carlquist 1965, 1966a, Cody & Overton 1996), and reduced dispersal ability in island plant species (Carlquist 1965, 1966b), further place strain on their adaptability to changing environmental conditions and ever increasing threats. Islands are described as nature's laboratories (Phillimore et al. 2008), with a host of endemic species, most of which occur only on single islands and are a conservation priority as a result (Biber 2002). Human introduced threats such as mammalian predators, over exploitation, habitat destruction and introduction of diseases, make island flora and fauna highly susceptible to extinction (Manne et al. 1999).

Humans have greatly altered island ecosystems over the past few centuries and through over-exploitation, habitat destruction, and the introduction of non-native species have negatively impacted a number of different island ecosystems worldwide (Pimm et al. 1994, Frankham 1998, Brook & Kikkawa 1998). Introduced pathogens and diseases coming from introduced species are also of great concern (Diamond 1984b, Groombridge 1992, Altizer et al. 2001, Dobson & Foufoupoulus 2001, Wikelski et al. 2012). With these threats causing reductions in populations, the threat of genetic factors causing further population declines, and eventually extinction become increasingly evident (Frankham 1998). Human-induced climate change is important to consider for future management, and conservation plans for protecting biodiversity on islands because of the predicted amplification of other threats that it is predicted to cause (Dobson & Carper 1992, Schneider et al. 1992; Hughes & Westoby 1994).

Research and conservation focuses on islands, and especially endemic island species, due to the negative impacts of threats often being greater on islands in comparison to the same threats in continental areas (Clavero et al. 2009). Conservation management of islands therefore needs to be proactive with frameworks that not only benefit the target species but are also advantageous for the broader ecosystem and other species within those systems (Morrison et al. 2011). Much focus is placed on single-species conservation on islands but increasingly the importance of protecting systems has become evident. This has been in part due to the recognition of secondary threats, such as environmental fluctuations and catastrophes (Brook & Kikkawa 1998), which impact islands on a broader scale. For example, Walsh et al. (2012) have shown that alien species, on islands where there are more endemic species, have a much greater impact on a wider suite of species than just the endemic species.

Island biogeography and extinction risk

Island biogeography theory predicts that larger islands house more species than smaller islands do (Simberloff 1976) because the small populations on islands have higher extinction rates (Simberloff & Wilson 1969). All other things being equal, species occurring on small islands are more likely to go extinct than those on larger islands (Simberloff 1976). Of course, all things are not equal, and extinction risk on islands has been greatly influenced by the history of human activities at specific islands (Pimm et al. 1994), and especially by the suite of species introduced by humans to islands (Manne et al. 1999).

The introduction of alien biota and direct exploitation of species is vital to consider when investigating the high number of extinctions of bird species on oceanic islands since 1600 (Pimm et al.1994). A disproportionately large number of historic bird extinctions have been flightless and island dwelling species (Hockey et al. 2011), largely as a result of the introduction of alien predators such as rats (Moors et al. 1992). Of the 108 extinctions of birds worldwide from 1600-1999, almost 90% have been of island species even though they make up only 20% of the world’s bird species (Frankham 1998). This highlights the need to, where possible; predict species responses to novel circumstances (Hockey et al. 2011). This is important for attempting effective remedial action preventing extinction or lowering extinction risk (Hockey et al. 2011).

Among terrestrial vertebrates, birds are the best colonisers of islands (Newton 2003), yet approximately 20% of birds are endemic to islands, highlighting the importance of conserving these areas (Gaston & Blackburn 1995). Island biotas, in particular island endemics, are highly vulnerable to the introduction of predators, competitors and diseases (Pimm et al. 1994, Manne et al. 1999). In most instances this is explained by species on isolated islands having been separated from mammalian or reptilian predators for a significant amount of time (Savidge 1987), in evolutionary terms, losing the anti-predator behaviour (Milberg & Tyrberg 1993, Duncan & Blackburn 2004, Blackburn et al. 2005) and resulting in higher susceptibility to introduced predators. The rapidity of some extinctions suggests a low level of resistance to any disturbance amongst island species (Hockey et al. 2011).

The loss of a number of island endemics on the Pacific island of Guam by the accidental introduction of the Brown Tree Snake (*Boiga irregularis*) is but one example of extinctions of oceanic island bird species (Savidge 1987, Fritts & Rodda 1998). Island-restricted species display extinction rates of more than 40 times the extinction rate of continental birds (Birdlife International 2008). This probably underestimates the losses of island birds already experienced, because many species probably have gone extinct undocumented (James et al. 1987, Milberg & Tyrberg 1993, Holdaway et al. 2001). With climate change becoming an increasingly important threat to these already vulnerable ecosystems, it would appear that the extinction risk of island species is set to increase over time (Benning et al. 2002, Gillespie et al. 2008).

Conservation efforts are often focussed on range-restricted species. The focus on species with very small ranges and single island endemics may be due to the majority of species that have been lost being single island endemics with small populations (Pimm et al. 1994). Characteristics of extinction-prone populations include a small initial population and a small geographic range (Diamond et al. 1987). Islands have some important single island small population species, and research efforts need to also focus on understudied areas and taxonomic groups (de Lima et al. 2011). The presence of single island endemics on Nightingale and Inaccessible Islands is largely due to the relatively pristine state of these systems and thus provides the ideal opportunity for research of natural systems.

General understanding of the decline and extinction of species is a main focus of the discipline of conservation biology (Thibault et al. 2002). Due to their smaller size and area of habitat, islands are a focal point of much research on endangered species (Thibault et al. 2002). The area of available habitat is often a good indicator of extinction risk (Trevino et al 2007, Gaston & Fuller 2009) and used by the IUCN as a classification criterion for threat status. Small disturbances such as environmental stochasticity that only slightly shift the balance between recruitment and mortality can dramatically increase the risk of extinction of a particular species (Brook & Kikkawa 1998). The impacts of stochastic events become magnified as populations decrease (Brook & Kikkawa 1998). It is therefore not unlikely that specialist species with smaller populations would be more threatened than generalists with larger populations (Brook & Kikkawa 1998). Long term management and monitoring, even of stable island populations, is vital to help prevent further extinctions (Brook & Kikkawa 1998).

The need for research in the South Atlantic region is highlighted by the presence of two critically endangered species on Gough Island (Tristan Albatross and Gough Bunting) and numerous other threatened species occurring on Tristan, Nightingale and Inaccessible Islands (Ryan 2007). A lack of knowledge on the two endemic bunting species that occur on Nightingale Island further provides reason for thorough research efforts in the region.

General background to the Nesospiza buntings

The *Nesospiza* buntings of the Tristan da Cunha Island group are one of the few examples of an adaptive radiation resulting from the arrival of a single ancestral group arriving at a group of oceanic islands (Lack 1947, 1971). *Nesospiza* buntings are seen as a classic example of a simple adaptive radiation (Lack 1947, Abbott 1978). Lack (1947) was one of the first scientists to contrast the *Nesospiza* radiation with the more extensive and well-known radiations of Darwin’s finches and the Hawaiian honeycreepers (Raikow 1976, Olson & James 1982, Grant 1999). The remote nature of the Tristan archipelago meant that it was only realised in 1922 that two different types of bunting occurred on the islands (Lowe 1923, Wilkin 1923). One advantage of being so remote is that the Tristan archipelago remains one of the least disturbed groups of islands in the temperate regions (Holdgate 1967, Wace & Holdgate 1976). However, this remoteness has meant that research on *Nesospiza* buntings in the past has been brief and mostly restricted to notes on their natural history (Hagen 1952, Elliot 1957, Richardson 1984).

An often overlooked aspect of conservation is that of maintaining evolutionary processes such as that of the radiation of *Nesospiza* buntings (Ryan et al. 2007). The origin of this complex is traced back to finch-tanagers (*Thraupini*) that reached the islands from South America (Rand 1955, Ryan et al. 2007). Traditional classification of *Nesospiza* included two species, each of which had different subspecies on Nightingale and Inaccessible Islands and a now extinct bunting that occurred on Tristan (Grant 2004, Ryan et al. 2007). Gough Bunting (*Rowettia goughensis*), endemic to Gough island, is the closest relative to the *Nesospiza* (Ryan 1992, Grant 2004). The colonisation of Tristan and Gough by buntings are suggested to be as a result of a single colonisation event (Jansen van Rensburg et al. 2012), although subsequent unpublished sequence data includes a wider range of potential ancestral species suggesting that Gough and Tristan do represent distinct colonisation events (P.G. Ryan, pers. comm.).

Within *Nesospiza* there are marked differences in size of the birds, especially in bill size, and this is related to different dietary preferences (Ryan 2008). The variety in morphology closely matches the suite of available seed sizes (Ryan et al. 2007, Ryan 2008). The revelation through research that morphological diversity evolved independently on each island lead to a revision of *Nesospiza* that recognised two species on Nightingale Island and a single, polytypic species on Inaccessible Island (Ryan 2008). Despite well-marked size variation on Innaccesible Island, the buntings there display high levels of hybridisation in certain areas (Ryan et al. 1994, Ryan 2001, Ryan et al. 2007), resulting in only a single species being recognised. Five different taxa were proposed, two on Nightingale Island and three on Inaccessible (Ryan 2008).

On Nightingale Island the speciation process appears complete, with a large billed specialist, Wilkins' Bunting (*Nesospiza wilkinsi*) and a small-billed generalist Nightingale Bunting (*Nesospiza questi*) occurring, with no records of hybridisation on the island (Delport et al. 2006, Ryan 2008). The island supports a single habitat; tussock *Spartina arundinacea* grassland interspersed with scattered Island Trees

Phylica arborea has favoured the evolution of two different taxa as a result of bimodal seed size distribution (Ryan 2008). The complexity of habitats on Inaccessible is possibly partly the reason for the complexity of taxa and high levels of hybridisation that exist (Ryan et al. 1994, Ryan 2001). Each of the taxa on Nightingale Island has a distinctive song and repertoire of calls and defends their territories primarily against conspecifics (Ryan et al. 2007). *Nesospiza* buntings are a clear example of ecological speciation where ecological processes appear to be largely responsible for driving the evolution and maintaining the diversity in morphology that is present (Ryan et al. 2007).

Other oceanic island archipelago bird radiations such as the Darwin's finches (Grant 1999) and Hawaiian honeycreepers (Raikow 1976, Olson & James 1982) are more extensive than the *Nesospiza* radiation. The Gough Bunting (*Rowettia goughensis*) is assumed to have shared a common ancestor with *Nesospiza* at some point in the past (Rand 1955, Grant 2004). The two genera were initially thought to have originated from separate colonization events and not due to island hopping (Rand 1955). More recent extensive sampling of potential ancestors in South America does suggest that these two genera evolved separately (P.G. Ryan, pers. comm.). Colonisation of each island took place once, followed by sympatric speciation when the bunting population had been established (Ryan et al. 2007). This sympatric speciation happened independently in each of the populations (Ryan et al. 2007). Strong directional selection along with genetic drift acting together would explain the two distinct and divergent bill sizes on Nightingale Island (Ryan et al. 2007).

The crushing force that seed-eating finches such as the *Nesospiza* complex can exert is directly proportional to bill depth (van der Meij & Bout 2006); consequently this determines the seed size they can exploit (Grant 1999, Grant & Grant 2002). Change in the width and depth of bills is usually indicative of alteration of function as displayed by the two different buntings on Nightingale Island (Grant 2004). In *Nesospiza*, bill size is highly heritable (Ryan 2001), and there is a close association between the bill depth of the birds and the seeds that are available within habitats (Ryan et al. 2007).

All *Nesospiza* species are threatened due to their highly restricted range and their vulnerability to the introduction of alien predators (Birdlife International 2008). However, among *Nesospiza* species, Wilkins' Bunting has the smallest population with low levels of genetic variability (Grant 2004), and is thus the most at risk of extinction and most susceptible to major disturbances (Ryan 2008).

The taxonomic decisions regarding the number of taxa and how many species of *Nesospiza* there are may dramatically impact conservation priorities (Ryan 2008). From a genetic perspective, should genetic variation within the species be related to the size of the population, a decrease in the number of Wilkins' Bunting on Nightingale Island could compromise the ability of the species to successfully adapt to any environmental changes in conditions (Frankham 1998).

Rationale and background to Wilkins' Bunting research

Wilkins' Bunting, the largest species of *Nesospiza*, is endemic to Nightingale Island. At less than 4km^2 this is the smallest of the three main islands in the Tristan da Cunha archipelago. It co-occurs with the Nightingale Bunting, the smallest of the *Nesospiza* buntings. Wilkins' Bunting is assumed to be a dietary specialist, feeding in close association with patches of the Island Tree (Ryan 2008). The highest density of the birds is to be found in the Ponds area, where most woodland occurs (Figure 2.1). Linked to its large body size, Wilkins' Bunting has the largest bill of any *Nesospiza*. This large bill has evolved to crack open the hard, nut-like *Phylica* fruits (Ryan 1992, Ryan et al. 2007). By comparison, the Nightingale Bunting has the smallest bill among *Nesospiza* taxa and is a generalist feeder targeting seeds of the tussock grass *Spartina arundinacea*, other small-seeded plants such as the various sedges as well as numerous small invertebrates (Ryan et al. 2007). As a result it is much more abundant than its larger relative, and occurs across the entire island (Ryan 2007).

Research on the populations and all aspects of the life history of these buntings in the past is scant due largely to the remoteness of the Tristan islands. Given its very limited habitat, Wilkins' Bunting has probably numbered fewer than 500 individuals for thousands of years (Ryan 2008). In the 1950s the population was estimated at 30 pairs (Elliott 1957) and Richardson (1984) estimated a similar population in the 1970s. In November 1999 further research that included the mapping of the *Phylica* on the island estimated the population to be approximately 50 pairs associated with an estimated 10 ha of suitable habitat (Ryan 2008). As a result the species qualified as Endangered under criterion D1 of the IUCN red list (Ryan 2008). A severe storm in

2001 damaged large areas of *Phylica* with subsequent day visits to the island yielding no sightings of the buntings. If the population had crashed there would be reason to classify the species as Critically Endangered in terms of criterion B1+3 (small range and fluctuating population) (Ryan 2008). It would seem that the affected areas of *Phylica* have exhibited substantial regrowth, and numerous buntings were caught and ringed in 2007 and 2009 (P.G. Ryan, unpubl. data).

With a total range of barely 1km^2 and an estimated population of 50 breeding pairs (and thus a total population of fewer than 200 individuals), Wilkins' Bunting is one of the most range restricted and small population bird species globally. Of conservation priority is a reassessment of the population size and to determine the population trend (Ryan 2008). Wilkins' Bunting is classified as endangered under the IUCN criteria due to its small range, population size and the continued threat of the introduction of alien mammals, such as has happened on Gough Island with severe effects on breeding success of several bird species (Cuthbert & Hilton 2004). A further threat is that of severe storms reducing the critical habitat of *Phylica*, such as the storm of 2001 that destroyed a large area of *Phylica* around the Ponds (Ryan 2008). Although little studied, alien scale insects appear to be causing reduced fruit loads on *Phylica* locally at Inaccessible Island (P.G. Ryan unpubl. data). A scale insect also has been reported from Nightingale Island (K. Herrian in litt.) raising concerns that a similar impact might be occurring at Nightingale Island. The importance of establishing a robust baseline for the population size, breeding success and survival of Wilkins' Bunting before the effects of the scale insect take hold is vital.

Very little is known about the breeding biology of Wilkins' Bunting (Elliot 1957, Ryan & Moloney 2002) making research on this aspect of the species vital to determine its ability to withstand the impacts of the abovementioned threats, particularly because of the highly restricted range of the species. Intensive studies on Inaccessible Island have shown that large-billed birds dependant on *Phylica* fruits in *Spartina/Phylica* habitat have much lower breeding success than the smaller-billed birds breeding in the same area that have a more generalised diet (Ryan 1992, Ryan & Moloney 2002). This may be offset by higher post-fledging survival of large-billed birds for which there is some evidence from Inaccessible Island (Ryan 1992, Ryan & Moloney 2002). Low breeding success however means that a small number of breeding pairs makes Wilkins' Bunting more susceptible to disturbance and genetic effects, which together could drive this species toward extinction.

Objectives of this study

This study provides baseline information on Wilkins' Bunting and the potential impact of introduced Greedy Scale (*Hemiberlesia rapax*) insects on *Phylica arborea*. Chapter 2 estimates the population size of Wilkins' Bunting on Nightingale Island by capturing and individually colour banding as many birds as possible. Resightings of marked birds allowed territories of breeding pairs to be mapped, providing a more robust estimate of the breeding population. Further objectives include determining aspects of foraging ecology, diet and behaviour through observation.

Chapter 3 focuses on aspects of *Phylica arborea* upon which Wilkins' Bunting is dependant as a key food source by recording fruit loads in trees, I test whether there are regional differences in fruit availability that might be correlated with bunting territory sizes. I also recorded the distribution of scale insects (*Hemiberlesia rapax*), where possible recording their abundance to assess whether these insects are impacting *Phylica* fruit loads on Nightingale Island.

Chapter 4 is a brief summary of the species' breeding biology, although the field season was unfortunately largely restricted to the pre-laying period.

The thesis concludes with a short synthesis summarising the key findings and making recommendations for future monitoring of this extremely small, vulnerable population. It is hoped that the Tristan Conservation Department will continue this monitoring into the future.

Chapter 2. Population size, territoriality and foraging ecology of Wilkins' Bunting

Introduction

Small populations with very restricted ranges, especially on islands, are highly susceptible to threats such as predation by alien mammals (Milberg & Tyrberg 1993, Pimm et al. 1994, Manne et al. 1999, Duncan & Blackburn 2007), which has lead to many island species going extinct (Halliday 1978, Fuller 1987, Blackburn et al. 2005, Hockey et al. 2011). Island endemics, in particular the more specialised species, make up a high proportion of currently threatened species of flora and fauna (Mountfort 1988, Johnson & Stattersfield 1990, Hockey et al. 2011) and of the species to have gone extinct from islands since 1600 (Manne et al. 1999, Hockey et al. 2011). Species with highly restricted ranges including island species, especially island endemics are often the species of greatest conservation concern today (Biber 2002). This is largely due to the high levels of endemism among island biodiversity. A further consideration is the negative impact humans have had on many islands (Pimm et al. 1994, Gaston 2002, Blackburn et al. 2005) and the need for conserving the remaining biodiversity and prioritising more pristine systems such as that of Nightingale Island, which forms part of the Tristan archipelago in the South Atlantic Ocean.

The Tristan archipelago has a number of endemic species, including six species of landbirds (Ryan 2007). Among these are three species of bunting (*Nesospiza*) that have radiated on the islands (Ryan et al.2007). Two of the buntings are confined to Nightingale Island: the more abundant, small-billed Nightingale Bunting (*N. questi*) and the scarce, large-billed Wilkins' Bunting (*N.wilkinsi*) that specialises on the fruit of the Island Tree *Phylica arborea* (Ryan 2007). Wilkins' Bunting is listed as Endangered on the IUCN Red list of threatened species (IUCN 2008). Although Nightingale Island is currently free of alien mammals, the constant threat of the introduction of rats or mice poses a potentially severe threat to these birds, as does the presence of a recently discovered scale insect on the *Phylica* trees (Ryan 2008). An introduced scale insect on Inaccessible Island in combination with a sooty mould (Crous et al. 2012) causes reduced fruit loads on *Phylica* trees (P.G. Ryan, unpubl. data). Consequently, a reassessment of the very small population of Wilkins' Bunting is a conservation priority (Ryan 2008).

Little is known about the foraging ecology, diet and territorial behaviour of the buntings on Nightingale Island. Wilkins' and Nightingale Buntings are thought to be highly territorial for at least the months of September through March (Ryan, 2007), but with few observations over winter it is unknown whether territories are maintained year round. Although it is widely accepted that Wilkins' Bunting, by the fact of the much larger bill size, is dependant on *Phylica* fruits (Lack 1947, Abbott 1978, Ryan 2008), there has been no systematic study of its diet, mainly due to the limited research opportunities on Nightingale Island to date.

Very little research has been conducted on the land birds of Nightingale Island (Hagen 1952, Elliott 1957, Abbott 1978). Three of the five terrestrial bird species endemic to the Tristan archipelago are found on Nightingale Island: the two buntings mentioned, and a subspecies of Tristan Thrush (*Hylocichla eremita*) (Ryan 2007). Gough Moorhen (*Gallinula comeri*) occurs only on Tristan, and the world's smallest flightless bird, the Inaccessible Island Rail (*Atlantisia rogersi*) is found only on Inaccessible, and has been the subject of some research over the years (Ryan et al. 1989, Fraser et al. 1992). Work on the Tristan Thrush, as with the buntings on Nightingale Island, is limited (Ryan & Moloney 1991, Fraser et al. 1994, Ryan & Ronconi 2010). The lack of research is due to the remoteness of this island and has lead to visits being short and infrequent (Moseley 1892, Wilkins 1923, Elliott 1957, Richardson 1984), and limited field studies (Fraser & Briggs 1992, Ryan & Moloney 2002).

The main objectives of the work described in this chapter were to gain a better understanding of the population size and number of breeding pairs of Wilkins' Bunting on Nightingale Island by catching and colour banding as many birds as possible during the field season, to map the territories of breeding pairs, focussing on the 'Ponds' area to determine densities of pairs in these areas, and to record the foraging ecology and diet of Wilkins' and Nightingale Buntings

Study area and Methods

Nightingale Island

The 2012 field season focussing on Wilkins' Bunting is one of the few extensive research efforts on the island and certainly one of the longest time periods, almost 3 months, for which researchers were permanently based on the island, providing an ideal opportunity to study this relatively pristine system. The smallest and oldest of the three islands of the Tristan archipelago, Nightingale Island has two nearby islets, Stoltenhoff and Middle (or Alex) Island (Figure 2.1). The highest point, known as High Ridge, in the eastern part of the island rises to approximately 400 m above sea level. The remainder of the island is mostly below 350 m (Baker et al.1964), but it descends steeply into the sea around much of the coastline. Middle Island is a low-lying islet rising to no more than 50 m above sea level and separated from Nightingale Island by a shallow channel approximately 300 m wide containing numerous rock stacks (Baker et al. 1964). Stoltenhoff is separated from Middle Island by a deeper channel some 600 m wide and comprises three rock stacks with sea cliffs up to 80 m high.

Nightingale Island is older and more eroded than the other Tristan islands, with rocks dating back some 18 million years, and consequently consists mainly of erosion resistant trachytes (Baker et al. 1964). There are no major drainage lines on the island, with the only standing water found in four small bogs known locally as “The Ponds” (Figure 2.2). There are a number of caves and rock stacks along the coastline, which is predominantly made of cliffs up to 120 m high (Baker et al. 1964).

Nightingale Island supports one major vegetation type dominated by tussock grass *Spartina arundinacea* with small patches of *Phylica* found mostly around the Ponds area and on High Ridge (Roux et al. 1992, Ryan 2007). The *Phylica* woodland community and *Blechnum palmiforme* heath, which is a vegetation of evenly spaced large ferns, together form the fern-bush vegetation type as described by Wace & Dickson (1965). Fern-bush is largely restricted to the Ponds area along with several areas of small bog grass *Scirpus bicolor*. Within the Ponds the dominant vegetation is that of Bog Ferns *Blechnum palmiforme* and large areas of floating *Scirpus sulcatus* (Ryan 1992). Middle Island has no *Phylica* present and is covered by tussock grassland but there is a small patch of woodland at the eastern end of the main stack of Stoltenhoff (Ryan 2008).

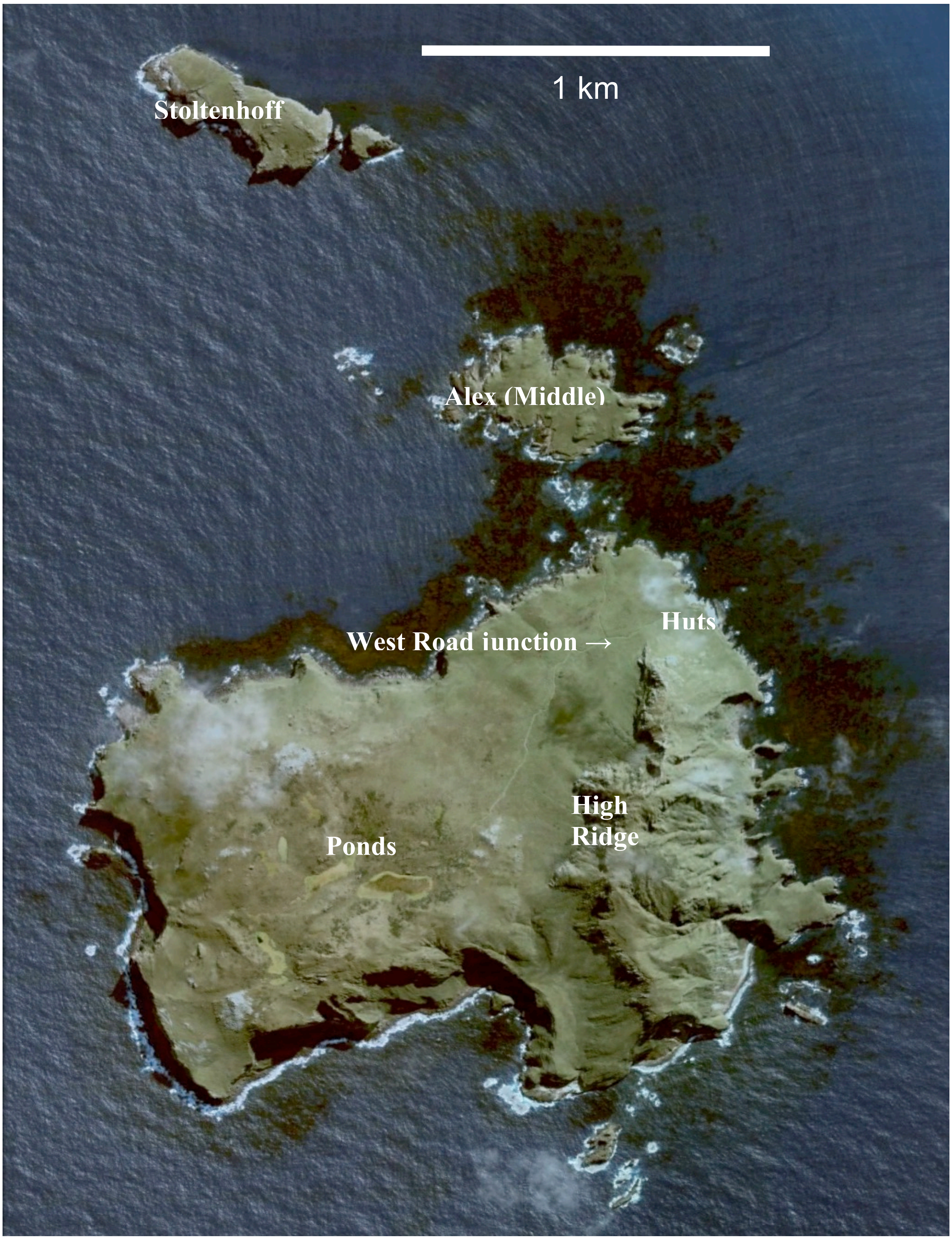

Figure 2.1: Google Earth image of Nightingale Island and neighbouring Alex (Middle) and Stoltenhoff Islands.

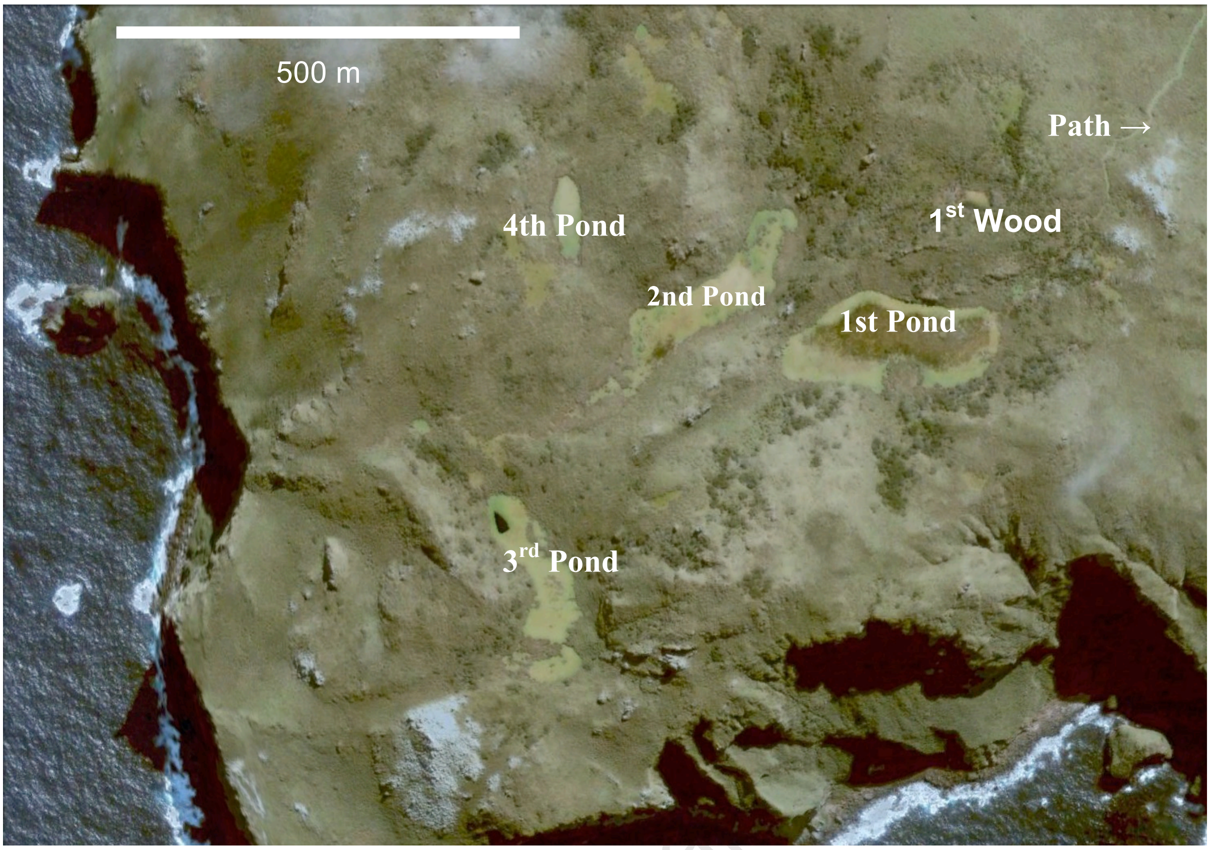

Figure 2.2: Google Earth image showing the four depressions known locally as 'The Ponds' surrounded by the majority of the island's *Phylica* patches (darker green).

Nightingale and Inaccessible are regarded as some of the best-preserved examples of temperate islands (Ryan et al. 2007). There are no introduced mammals on either island, but Black Rats *Rattus rattus* and House Mice *Mus domesticus* occur on the main island of Tristan (Wace & Holdgate 1976, Ryan 2007). For this reason, it is important to have strict quarantine measures in place and to regularly check rodent traps put out around landing sites on Nightingale Island. Mice or rats could cause extensive and irreversible damage to seabird populations on the island, as has occurred on many islands (Moors et al. 1992), especially in the Pacific Ocean (Pimm et al. 1994, Thibault et al. 2002). Nightingale Island, although often visited by humans, remains less disturbed than Inaccessible and Tristan largely due to the lack of potable water (Wace & Holdgate 1976, Ryan 2007).

Catching, measuring and ringing buntings

I visited Nightingale Island from 14 September to 26 November 2012. Wilkins' Buntings were caught by using mist nets, mostly for territorial pairs, and hand nets to pursue single birds, generally for birds foraging in tussock grassland or on the ground in fern-bush woodland. The use of hand nets proved especially productive for catching immatures and in areas where mist nets were not feasible. Up to four mist nets at a time, two 6 m and two 9 m nets, were erected in between patches of *Phylica* trees. Recordings of the calls of Wilkins' Bunting and Nightingale Bunting were played at the base of the mist net using an MP3 player to attract birds into the nets. Territorial interactions between pairs of Wilkins' Bunting only became more apparent and frequent from mid-October, rendering this approach not very successful for the first month. In certain areas, such as the *Phylica* surrounding 3rd and 4th Ponds, mist nets were not used at all and only hand nets were used to catch birds.

The following variables were recorded for each captured bird for both Wilkins' and Nightingale buntings: total head length, bill depth (measured vertically at the proximal edge of the nares), tarsus (all to the nearest 0.1mm), tail and wing (using a stopped wing rule, flattened chord to the nearest 1 mm) as in Ryan (2001). Each bird was individually aged and sexed. Birds were either classified as adult or immature. Immature birds were identifiable by heavy streaking on the nape and back and were drabber and paler overall (Ryan et al. 1994, Ryan 2007). Sexing of adult birds was based on the overall colouration of the birds (Ryan et al. 1994). Male birds are overall a brighter yellow green with almost no streaking on the back, and have a heavier and darker bill. Males were also identifiable by their singing. Females are more streaked on the nape and back, and are overall not as bright yellow green as the males.

All buntings were banded with a metal ring with a unique code on the right leg to distinguish birds from those ringed in 2007 and 2009, which had rings on the left leg. Nightingale Buntings were ringed with 2.8 mm F-series rings (de Beer et al. 2001) and Wilkins' Buntings either 3.5 mm C-series rings or 4.2 mm 4-series rings (de Beer et al. 2001). Individual combinations of three 4.5 mm colour bands (eight colours) were placed onto every Wilkins' Bunting captured. For Nightingale Buntings, only birds caught along the paths between the huts and the West landing, inland to the West Road junction were individually marked with colour bands (diameter 2.8 mm).

Plastic colour bands were deployed one above the metal ring on the right leg and two on the left leg (see Appendix 1, Table 1). To reduce the likelihood of confusion, the same two colours on the left leg were not used in reverse order (e.g. red over green and green over red), unless a pair was caught together. Colour bands were sealed with a spot of super glue and by the end of the field season no bird was observed to have lost colour rings. The location of capture for each individual was recorded with a GARMIN GPS 60.

Territory size estimation

Marked buntings were resighted as often as possible and GPS co-ordinates recorded for all sightings, noting behaviours such as territorial interactions with neighbouring pairs. These interactions were characterised by loud chattering vocalisations and birds chasing and attempting to bite other buntings in more aggressive instances. All observation positions were viewed in Google Earth to ratify the accuracy of these recordings and added as layers to ArcGIS 9.3 (using the WGS 84 geographic co-ordinate system). I then re-projected all the layers onto the UTM 28S co-ordinate system to enable more accurate calculations of territory areas. Minimum convex polygons (MCP) were used to estimate the area of each territory (Rodgers & Carr 1998), which requires at least three data points. I used Hawth's Analysis Tools package (Beyer 2004) to analyse the territories and create the MCPs. Only territories for colour ringed pairs and pairs with metal rings from previous years that could be differentiated from neighbouring pairs were included in the analysis of territory area.

I used a one-way ANOVA, incorporating the variables of site (referring to the five areas) and the size of the indivivudal territories within these areas,to test for significant differences between sizes of territories in five different areas: 1st Pond, 2nd Pond, 3rd Pond, 4th Pond and 1st Wood (Figure 2.3), with a *post hoc* Tukey test used to see which sites differed. I also compared territory sizes around the Ponds with those in 1st Wood with a t-test.

Foraging ecology and diet observations

Opportunistic observations of foraging behaviour and diet observations were made for both Wilkins' and Nightingale buntings, following focal birds during territory mapping and during observations for nest building. Foraging location was allocated to one of three habitats: in *Phylica* trees, on the ground in woodland and fern-bush habitat, and in tussock grassland. Information recorded included the species of plant on which the birds fed and, in the case of insects/invertebrates, the species was recorded when it was clearly identifiable otherwise recorded as 'insects.' Invertebrates were collected to help identify the 'insects' eaten by both species of bunting.

Results

Bunting measurements

The bill depth of Wilkins' Bunting (average >14 mm) was almost twice that of the Nightingale Buntings (Table 2.1). In both species, males averaged larger than females. Some female Wilkins' Buntings toward the end of the field season had an unusually high mass (e.g. 59.5 grams), and probably were developing eggs, otherwise females were generally lighter than males. There was no evidence of intermediate-sized hybrids between the two species (cf. Ryan et al. 1994, Ryan 2001, Ryan & Moloney 2002), nor were any such birds observed in the field season in 2012.

Table 2.1: Mean measurements of Wilkins' and Nightingale Buntings caught on Nightingale Island in 2012. Numbers in parentheses indicate ranges.

	Head length (mm)	Bill depth (mm)	Wing (mm)	Tarsus (mm)	Mass (g)
Wilkins' Bunting					
Male (n=55)	43.4 (41.7-45.0)	14.7 (13.8-15.1)	99.0 (93.0-102.8)	28.3 (25.9-30.0)	53.1(45.0-56.7)
Female (n=58)	42.1 (40.6-43.9)	14.1 (13.6-14.8)	95.5 (92.0-98.5)	27.5 (26.0-29.4)	51.1 (46.0-59.5)
Nightingale Bunting					
Male (n=63)	35.1(32.7-37.0)	7.8 (7.2-8.5)	82.4 (76.5-88.0)	23.8 (21.2-26.6)	27.6 (25.1-29.6)
Female (n=59)	34.5(32.4-36.3)	7.4 (6.8-8.5)	79.4 (75.0-84.5)	22.9 (21.5-25.6)	25.7 (21.4-29.0)

Foraging ecology and diet

There was a significant difference in the foraging areas of adult versus immature Wilkins' Buntings (Figure 2.3, $x^2 = 13.82$, df = 2, $p < 0.001$). Adults were found mostly in *Phylica* trees (51%) whereas immature birds mostly foraged on the ground in fern-bush habitat (62%). Immature birds were seldom observed foraging in tussock grassland (4%), much less than adults.

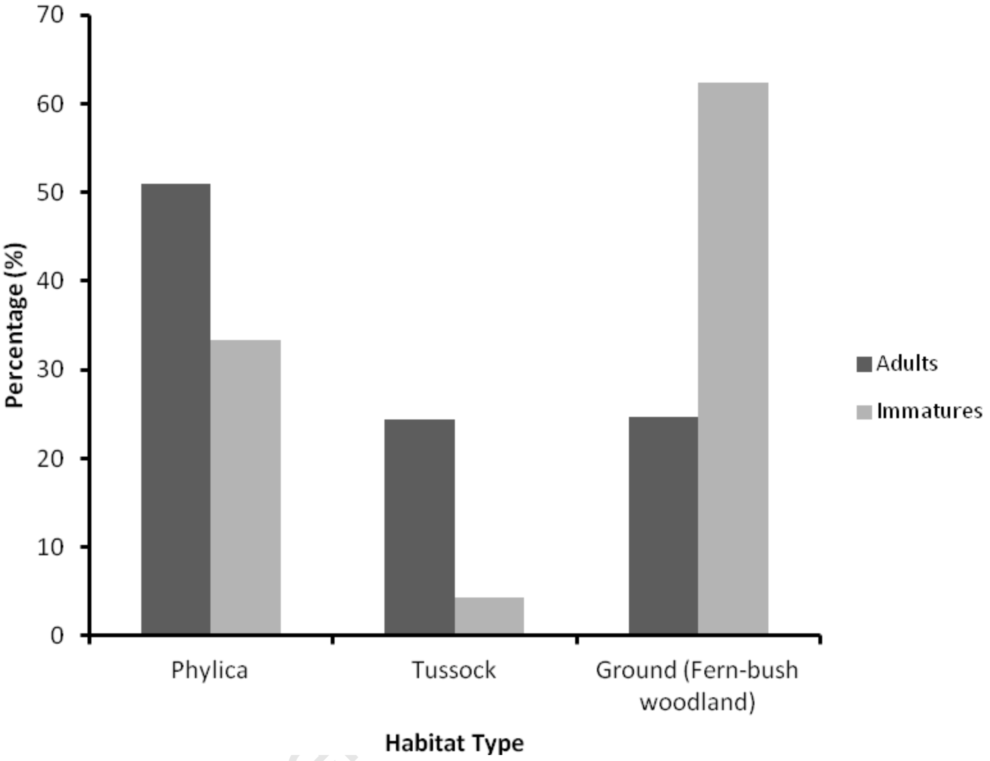

Figure 2.3: Percentage of observations of adult and immature Wilkins' Buntings in each category of habitat during the field season of 2012. The total number of adult observations (n=292) and observations of immatures for which data was recorded (n=69).

Territory size

The average territory size of the 55 pairs of Wilkins' Bunting was 0.149 ± 0.093 ha. The largest territory recorded was that of a pair of buntings on the eastern side of 1st Wood that had an area of 0.34 ha, and the smallest mapped territory was at the south western edge of 1st Pond with an area of 0.012 ha. The total area for the 55 mapped territories was 7.6 ha. As expected this is less than the 10 ha of *Phylica* on the island recorded by Ryan (2008) as not all areas were included in this calculation. No territories along the path (not enough data points for MCP construction), and no territories from High Ridge (only two visits) were included in this calculation.

Local variation in territory size

The *post hoc* Tukey test, suggested that territory size differed in three pairs of areas (Figure 2.4). There was no statistical support for evidence in Figure 2.4 that 4th Pond territories were larger than 1st and 2nd Pond territories. The core area of *Phylica* is centred around the 'Ponds' and to the western plateau of the island (Figure 2.5). The remaining area of the island is dominated by tussock grassland. This gives an overall density of 7.2 pairs.ha^{-1} (Range 5.7 pairs.ha^{-1}, 15.3 pairs.ha^{-1}) in *Phylica* woodland around the Ponds. By including the immatures (n = 28), all caught within these territories, the density increases to 9.1 pairs.ha^{-1}.

According to the post hoc Tukey test, 4th Pond territories were found to be the largest at 0.205 ha, however they differed significantly only from 3rd Pond territories (p = 0.011), which were the smallest territories (0.065 ± 0.05 ha, ANOVA $F_{1,4} = 5.81$, p = 0.002). 1st Wood territories, the second largest at 0.2 ± 0.1ha, were found to be larger than 3rd Pond territories (p-0.006). 2nd Pond territories were larger than 3rd Pond areas (p=0.048). From the figure 4th Pond territories appear larger than other "Pond' areas.

Population size and structure of Wilkins' Bunting

A total of 114 Wilkins' Buntings was caught (Table 2.3): 86 adults and 28 immatures. The sex ratio was roughly equal: 55 males (43 adults, 12 immatures) and 58 females (42 adults, 16 immatures). Only 10 Wilkins' Buntings were not resighted after being colour banded. At least 12 Wilkins' Buntings were observed that were already banded, of which five were recaptured. Four were caught as adults in 2007 (of 29 adults banded that year) and the fifth as an adult in 1999 (of 15 adults banded that year), giving a minimum age of 13 years. This bird was however not resighted. All five birds were caught in the same area where they were caught 5-12 years previously.

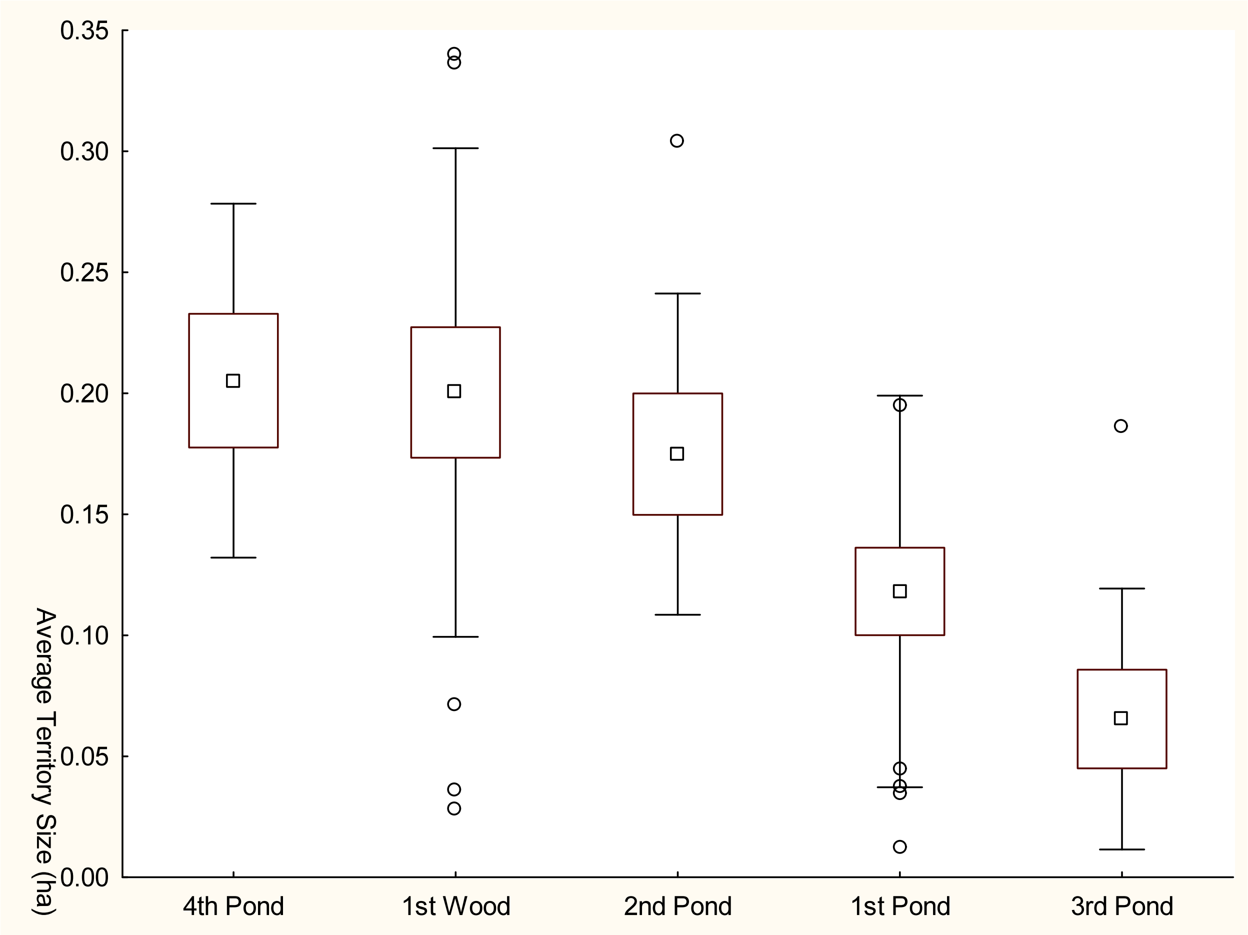

Figure 2.4: Box and whisker plot of the average territory sizes for the five different areas sampled on Nightingale Island in order of ranked means. The mean values, maximum and minimum values (excluding outliers) and ranges for each region are displayed.

Five unringed Wilkins' Buntings were observed during the last two weeks of the field season. As these birds were seen singly it would suggest that they might be floaters that do not have a territory. The numbers in parentheses in Table 2.3 provide an upper and lower bound for estimates in cases where there remains uncertainty as to the actual number of birds in those particular categories.

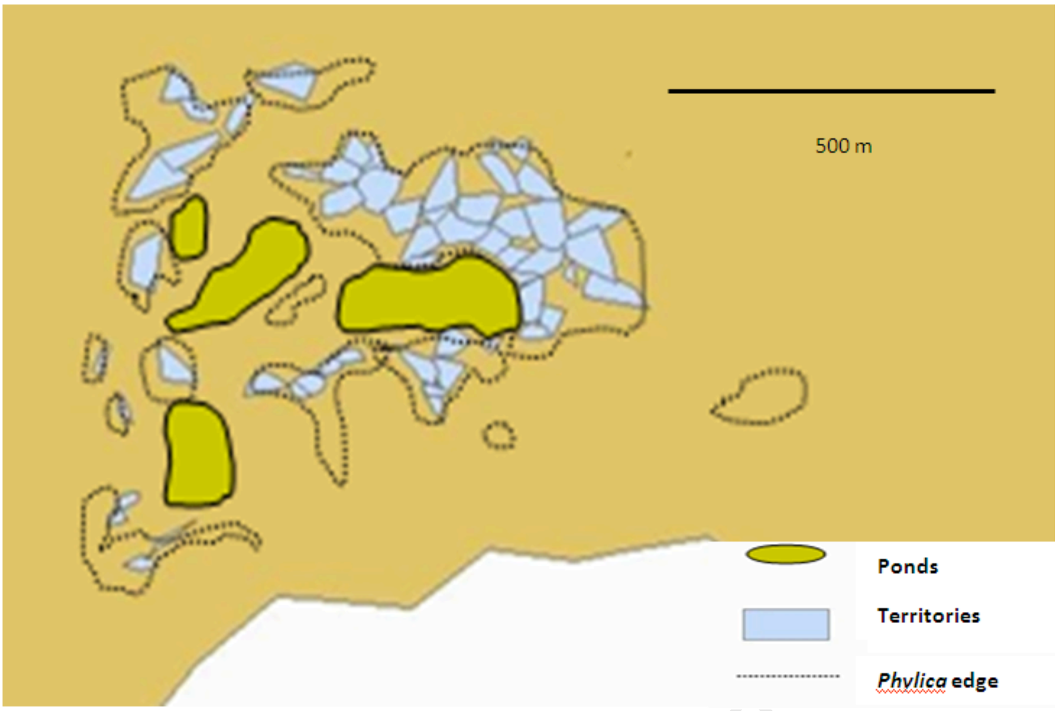

Figure 2.5: Territories of 55 marked pairs of Wilkins' Bunting around the Ponds on Nightingale Island. The sample area is displayed as the dashed line around the territories.

Table 2.3: Number of birds with colour bands; estimated population size and demographics of the population of Wilkins' Bunting

Description	Total
Ringed pairs (pairs with at least one bird colour banded)	56
Unringed pairs (including previously banded birds*)	25 (22-28)
Estimated number of breeding pairs	80 (75-85)
Total birds caught and colour banded	114
Estimated population size (minimum)	216
Estimated population size (maximum)	250

*Note: this includes an estimation of 8-10 pairs of Wilkins' Bunting in the High ridge area. Numbers in parentheses show the possible range for each parameter.

By the end of the 2012 field season at least one bird of 56 different pairs had been colour banded (Table 2.3). Immature birds represented just less than 25% of all birds captured. Three unringed immatures were observed during the last two weeks of the field season and not captured. Two immature birds were observed with their presumed parents in September until early October. By mid-October these birds were no longer observed with the adult birds, and subsequently were seen foraging on their own outside of the adults' territories.

The broad range for the estimated population size is due to uncertainty around the numbers of buntings in certain areas, especially along High Ridge. I estimated a minimum of 75 pairs of buntings and a maximum of 85 pairs, as I recorded through the field season 81 pairs without taking into consideration parts of High Ridge for which extrapolations would be difficult. The minimum number of pairs is less than 81 as I may have counted unringed pairs twice as they are not individually identifiable. When considering only these birds the population is between 150 and 170 birds. By including the extra immatures and single adults, the 6 to 8 extra pairs on High ridge, the 39 banded birds not part of the breeding pairs accounted for and the 150-170 birds in breeding pairs; the total population is between a minimum of no less than 216 birds and probably not more than 250 birds in total. The uncertainty around certain numbers of buntings is quite high as not all areas on the island were extensively covered, with some areas being visited only once, increasing the likelihood of missing birds that are in fact present in those areas.

Discussion

Bunting measurements

On Nightingale Island, the evolution of two different taxa of *Nesospiza* buntings has been favoured by the presence of a bimodal seed size distribution (Ryan 2008). This is in contrast to Inaccessible Island where the buntings have a range of bill sizes, which correlate to the range of seed sizes on the island (Ryan 2001, Ryan et al. 2007). Variation in beak sizes in other finches, such as on the Galapagos Islands, has been attributed to the preference for differing proportions of the available seed range (Grant et al. 1976, Abbott et al. 1977, Grant & Grant 1996). The differences between Wilkins' and Nightingale Buntings are highlighted in Table 2.1, in particular between bill depths of the two species. Furthermore, the absence of intermediate measurements for birds and no observations of birds exhibiting a mixture of features during an 11 week field season in 2012, suggests that no hybrids occur and supports the concept that speciation is complete on Nightingale Island (Ryan 2008). The presence of two distinct species may be as a result of the clear distinction between the size of *Phylica* seeds, which are much larger and fed on by Wilkins' Buntings, and the smaller seeds of *Spartina*, *Carex* spp and other smaller seed species that the Nightingale Buntings feed on.

The bill depth of these two species, as in other seed-eating finches, is directly proportional to the crushing force they can exert (van der Meij & Bout 2006) and consequently determines the size of seed they can exploit (Grant 1999, van der Meij & Bout 2006). The larger and harder seeds of the *Phylica* trees require a greater crushing force to be successfully cracked open. This helps explain the much larger bill of the Wilkins' Bunting and has lead to the description of this species as a specialist feeder heavily reliant on these seeds as a source of food (Ryan 2008). The fact that the seeds are available year-round makes the selection for a larger bill advantageous.

The larger general body size of the Wilkins' compared to Nightingale Buntings is clearly shown by the comparative wing lengths, head size, and mass of the birds with Wilkins' birds consistently twice as heavy (ca 50g) as Nightingale Buntings (ca 25g) (see also Table 2.1). One can infer that this distinct difference in body size is driven by the different dietary preferences of these two species. Correlations between bill size and head size in other seed eating finches (van der Meij & Bout 2004, van der Meij & Bout 2006) would suggest that diet has been a major driver toward the two distinctly different body sizes, including head size, of these bunting species.

Foraging ecology and diet

Adult and immature Wilkins' buntings prefer to forage in different areas of the same broad habitat type (Figure 2.3). A significant difference (Figure 2.3) in foraging behaviour was recorded between adults and immatures across all three habitat types. Adults preferred to forage in the *Phylica* trees on ripe fruit whereas the immature birds were most often encountered feeding on the ground, on fallen *Phylica* seeds and invertebrates. By observing interactions between adult and immature buntings, immatures prefer to feed on the ground within the fern-bush habitat to avoid harassment by adult birds with territories, particularly males, toward the onset of the breeding season. Immatures were chased out of territories if seen by the local pair, and on one occasion, the immature bird was bitten by both adult birds in a scuffle on the ground. The two most intense interactions observed both involved immature male birds being chased, one of which was observed calling toward the end of the field season, but still had immature plumage.

In certain areas, such as the 'right fork wood' of 1st Wood, groups of young birds (3 to 5) were at times observed foraging together. These birds preferred to forage on the ground in an area between two territories of adult birds. There is a sufficient amount of fallen *Phylica* seed on the ground at this time of year in this habitat for the immatures to be able to survive, without having to feed often in the tree canopy where they are more likely to be chased by adult birds. Through the entire field season I did not observe any similar behaviour of adult birds forming groups, although single adults that did not hold territories did on occasion join the group of immatures in 1st Wood.

Based largely on limited observations in the past, it has been inferred that Wilkins' Buntings are largely reliant on *Phylica* seeds and that it is the main constituent of their diet. The 2012 field season revealed that *Phylica* seeds are indeed a vital part of their diet as observations of birds feeding on the ground also showed a preference for fallen seeds of *Phylica*. Birds were observed to bite at the bark of *Phylica* trees and bite at old tussock stalks, possibly for invertebrates. There is a high prevalence of alien weevil beetles (*Stenoscelis hylastoides*) in the old branches and twigs of the *Phylica* trees and this would seem to be one species that the buntings feed on by breaking off twigs.

Nightingale Buntings were observed feeding on the following species: *Carex insularis*, *Carex thouarsii*, *Scirpus bicolor*, *Scirpus sulcatus*, and the alien grass *Poa annua* as well as both species of Brass button, the indigenous *Cotula moseleyi* and the non-native invasive *Cotula australis*. Nightingale Buntings that were observed in *Phylica* trees were seen to be gleaning invertebrates off moss and lichens as well as the undersides of the leaves and were not seen to feed on *Phylica* at all. From these observations it is clear that these two species occupy quite distinct niches in terms of diet. Due to the late flowering of tussock grassland I was unable to determine if both species feed on this species as no seed had been set by the end of November.

Territory size

The size of territories is to a large degree determined by the net costs and benefits present (Fretwell & Lucas 1970, Both & Visser 2003). Smaller territories are expected to have a higher abundance of resources (Fretwell & Lucas 1970); on Nightingale Island this would relate to higher *Phylica* fruit loads in these areas. The high density of bunting pairs on Nightingale Island would suggest relatively small territory sizes and the variation in density across the different regions would suffice to suggest that there is variation in the sizes of territories across the different regions of the island.

It was not possible to accurately map the territories for all pairs across the island during the 2012 field season and therefore the focus of the field season was around the Ponds area of the island (Figure 2.5). Differences in mean territory size were found to not be significant for a number of areas (Figure 2.4). 3rd Pond has smaller territories than 1st Wood, 2nd Pond and 4th Pond (Figure 2.4). This may be due to the small and relatively isolated patches of *Phylica* in the 3rd Pond region.

The intruder pressure hypothesis and the optimal territory size models predict an inverse relationship between territory size and resource density (Marshall & Cooper 2004). Therefore, 3rd Pond territories should display the highest fruit loads of *Phylica*, as these are the smallest territories on the island (Figure 2.4). However, it is worth noting that the naturally smaller patches of *Phylica* in this area probably also plays a role in controlling territory size. 1st Wood territories are conversely much larger for the same reasons, as the *Phylica* there is largely continuous and unbroken when compared to other regions. The lack of significant difference between 1st, 2nd and 4th Pond territories could be explained by the similarity in habitat structure, and the close proximity of these areas to each other, whereas 3rd Pond is in a localised SW corner of the island furthest away from the others. The large variability in size of the territories across the 3 different Ponds could also help explain why statistically one cannot determine significant differences between the three.

Breeding pair densities in the different regions

The overall density of breeding pairs in the mapped areas was 7.24 prs.ha^{-1} (Table 2.2). This relatively high density is expected based on the fact that only approximately

10 ha of *Phylica* exist on the island (Ryan 2008) and the estimated population is approximately 200 birds, which would relate to 20 birds per hectare or a maximum of 10 prs.ha^{-1}. The overall average density may be higher than the recorded 7.24 prs.ha^{-1}. This could be investigated with more research by determining more accurate figures for the number of pairs on High Ridge and other isolated patches of *Phylica*. This is supported by the fact that, when one adds the immatures the density increases to 9.1 pairs.ha^{-1}. The presence of 3 pairs just above the huts, where only a few *Phylica* trees occur, would suggest that most, if not all, small patches of *Phylica* would contain pairs of buntings and therefore increase the actual density across the island.

The variation in density of birds for the different areas of the mapped region is substantial, with the 3rd Pond region having 15.3 prs.ha^{-1} compared to the lowest density around 4th Pond of 4.6 prs.ha^{-1}. The 3rd Pond region is characterised by small, disjoint patches of *Phylica* woodland with no single large continuous strip of woodland being present such as in parts of 1st Wood and the other Ponds. Without a comprehensive study of factors such as fruit loads in this area, and other variables that may explain the higher density, it is difficult to pinpoint the reasons for this much higher density. It may be that pairs are only able to defend single patches and because these are smaller in 3rd Pond, it results in smaller territories and higher densities per hectare of *Phylica* woodland present in the area.

Population size and structure

Prior to this particular field season the estimated population for Wilkins' Bunting was approximately 200 birds with about 50 breeding pairs (Ryan 2008). A positive finding from this study was the higher number of pairs found on the island (Table 2.3). The current estimate of between 75 and 85 pairs is up to 60 % more than the previously estimated 50 pairs (Ryan 2008) of Wilkins' Bunting on the island. With pairs being found in all the patches of *Phylica* that were regularly visited during the field season, it seems that, due to the limited extent of habitat available, the population may not get much larger. Some work is being done by the Tristan Conservation Department to plant seedlings of *Phylica* in patches being overgrown by tussock grassland, but this will take at least a decade before these trees provide sufficient fruit to support more pairs of Wilkins' Buntings.

Single island endemics are very susceptible to extinction (Milberg & Tyrberg 1993, Pimm et al. 1994, Biber 2002, Duncan & Blackburn 2007) and highly localised with very small population sizes. The small population factor brings with it a suite of problems, such as the Allee effect and genetic diversity problems, such as low levels of heterozygosity (Frankham 1996). Wilkins' Bunting would appear to have been a very small population species for a long period of time (Ryan 2008). Based on observations and buntings captured throughout the field season, the revised population estimate is up to approximately 250 Wilkins' Buntings on the island (Table 2.3). Although higher than previous estimates, it is concerning that the population estimate is not also larger. This may be due to the relatively low number of immature birds captured. With up to 85 pairs of buntings present, one could expect a higher proportion of immatures in the population. The low number of immatures (n = 28) caught may be purely due to territorial adult birds being easier to catch, or as a result of a high survival rate. However, without any thorough research that provides sufficient information regarding breeding success and post fledging survival, any conclusions made at present remain speculative.

Further surveys of Wilkins' Bunting focussing on areas such as High Ridge in the eastern parts of the island are required to improve accuracy of current population estimates. These are currently based on extrapolations from a few patches of *Phylica* at the far southern edge of High Ridge. Due to the limited extent of available habitat it is unlikely that the population would increase to levels much higher than at present, unless the fruit load remains unaffected by the scale insect and current densities are below carrying capacity.

Chapter 3. Does the introduced scale insect *Hemiberlesia rapax* (Comstock) affect the abundance of *Phylica arborea* fruit on Nightingale Island? Implications for Wilkins' Bunting

Introduction

Phylica is a large genus of some 150 species of shrubs and small trees. Most species are confined to the Cape floristic region of South Africa, with other species in eastern South Africa, Zimbabwe, Malawi and Tanzania (Richardson et al. 2001). Five species are confined to oceanic islands: Reunion, Mauritius, Madagascar, Amsterdam, St. Helena, the islands of the Tristan archipelago and Gough Island (Richardson et al. 2001) The Island Tree *Phylica arborea* occurs not only on Tristan and Gough in the central South Atlantic Ocean, but also Amsterdam Island in the south-central Indian Ocean (Richardson et al. 2001). Its ability to disperse long distances is impressive, considering the fruits and seeds are not typical of long distance dispersal types (Richardson et al. 2003). Island species of *Phylica* are morphologically as well as genetically distinct from the mainland species (Richardson et al. 2003).

Nightingale Island is dominated by tall, dense tussock *Spartina arundinacea* grassland. This dense vegetation hinders the successful germination and establishment of young *Phylica* seedlings (Dean et al. 1994). As a result, there are scattered patches of *Phylica* across the island with the largest area of these trees occurring around the 'Ponds' (Figure 2.2). More isolated patches of *Phylica* are found on High Ridge and along the path above the huts. *Phylica* patches are the critical habitat for Wilkins' Bunting, which are largely dependant on *Phylica* fruit (Chapter 2). The discovery of a suspected introduced scale insect (K. Herian, in litt.) is cause for concern, because data from Inaccessible Island suggest that *Phylica* fruit loads can be severely impacted by the presence of scale insects (P.G. Ryan, unpubl. data). On Inaccessible, the Soft Brown Scale (*Coccus hesperidum*) is found in association with a black sooty mould fungus *Seiridium phylicae* (Crous et al. 2012). The discovery of scale insects on Nightingale Island raises concerns about their potential impacts on Wilkins' Buntings (Ryan 2008).

The impacts of scale insects on host plants vary considerably. Some studies show that plants can compensate for some negative impacts by herbivores such as scale insects through physiological alterations (Oleksyn et al. 1998, Anten & Ackerly 2001, Thomson et al. 2003, Retuerto et al. 2004). Retuerto et al. (2004) showed an increased rate of photosynthesis in response to increased scale abundance. However, high densities of scale insects on Pinyon Pines (*Pinus edulis*) caused severe chlorosis and premature needle shedding (Gehring et al. 1997). Other impacts include canopy dieback and even death of some trees (O'Dowd et al. 2003). Scale insects also can predispose trees to fungal infection (Harvell et al. 2002) as is evident on Inaccessible Island (Crous et al. 2012) with resultant impacts on *Phylica* fruit loads (P.G. Ryan, unpubl. data). If this occurs on Nightingale Island it could threaten the survival of Wilkins' Buntings.

This chapter reports the abundance and distribution of the scale insect *Hemiberlesia rapax* (Comstock) on *Phylica* trees on Nightingale Island and estimates local and regional variation in *Phylica* fruit loads. By comparing fruit loads of healthy trees to trees infested with scale insects, I should be able to assess the impacts of scale insects on *Phylica* fruit loads. I also searched for signs of a fungus such as the sooty mould found on Inaccessible Island.

Materials and Methods

Phylica *fruit loads*

Fruit abundance on *Phylica* trees was estimated around the Ponds by sampling up to 20 large trees in Wilkins' Buntings territories across the island, and was also estimated along each of the four transects carried out across the island. As many large trees as possible were sampled in peripheral territories with fewer trees. Saplings and young trees (basal circumference <15 cm) were not sampled because *Phylica* only starts to bear typical fruit loads above this size. As many territories surrounding the Ponds (Figure 2.5) as possible were sampled and territories from other areas were sampled on an *ad hoc* basis in order to establish whether there was any local variation in fruit load. The basal circumference of each tree sampled was measured to the nearest 1 cm with a piece of string. The height of each tree was estimated to the nearest 0.1m using a 2.5 m net pole.

Fruit load was determined, for each territory and along the four transects, initially by assigning a qualitative score to each tree on a scale of 0 to 5: 0 = no fruit (0 fruit per branchlet), 1 = very few (1-5), 2 = some (6-10), 3 = average (11-15), 4 = above average (16-20) and 5 = lots of fruit (>20 per branchlet). A branchlet was classified as the terminal 15 cm of an exposed branch (10-15 cm wide). This qualitative scale was applied after having spent some time working with the trees to gain a better understanding of average fruit loads. In order to provide a more quantitative index of fruit abundance, 10 terminal branchlets were selected from each tree and the number of fruit counted (individually for counts <20, estimated to the nearest 5 when n>20).. Branchlets were selected from different parts of the canopy for each tree to ensure representative sample coverage of each tree and thus reduce any sampling bias.

I compared the average fruit load per tree in each Wilkins' Bunting territory to determine whether there was any local variation. The 24 territories analysed were initially broadly categorised into Ponds (n=20, incorporating the periphery of 1st, 2nd and 4th Ponds) versus sites that were in areas away from the Ponds, such as 1st Wood and along the path near the huts (n=4).The second set of analyses treated each Pond separately. An ANOVA was run with a *post hoc* Tukey test to determine which interactions differed statistically. The variables incorporated into this statistical analysis were the five different areas e.g first Pond, and the response variable of average fruit load per territory. This interaction analysis allowed for comparison between the different Ponds as well as with other regions where fruit load had been counted in specific territories. All statistical analyses were conducted in the R Studio statistical package (RStudio 2012).

Comparative data for the fruit loads of *Phylica* trees from comparable habitat near Blenden Hall in the lowlands of Inaccessible Island were available (P.G. Ryan, unpubl. data). These data have not yet been used in any publications but are useful to compare the impacts of scale insects on trees on the two different islands as well as looking into differences between fruit loads on the two islands. The means for fruit loads of healthy trees from Inaccessible were compared to trees from Nightingale Island in the 24 territories for which fruit loads were recorded.

Scale insect distribution and abundance

The distribution of introduced scale insects on the island was mapped by recording GPS co-ordinates, with a GARMIN GPS 60 device, in as many areas of *Phylica* woodland as possible (between 14 September and 26 November 2012). Scale insect abundance was scored from 0-3: 0 = none, 1 = very few, 2 = moderate and 3 = heavy infestation, within each territory and along each of the four transects carried out across the island. In instances where trees exhibited varying numbers of scale insects on different terminal branches I assigned 1-2 or 2-3. Within each territory for which fruit loads were counted, the presence of scale insects and their overall abundance was recorded.

The same procedure used to map the territories of Wilkins' Bunting pairs (Chapter 2) was used to map the distribution and abundance of scale insects in ArcGIS 9.3. The shapefile 'scale' comprises point data (individual trees sampled) and polygon data (summary data per bunting territory).

In 19 Wilkins' Bunting territories from the fruit load study I also recorded if each tree had scale insects present. After pooling fruit loads with and without scale insects across the 19 different territories, I used a t-test to determine if the presence of scale insects affected fruit loads. The analysis was compared to that of trees on Inaccessible Island for which comparable data were available (P.G. Ryan, unpubl. data).

Four 50 m transects (one comprising two separate 25 m transects due to the limited extent of woodland) were carried out, determining the presence of scale insects on trees along the transect. One transect was carried out on the periphery of each of the four Ponds. The two 25 m transects were done in woodland along the periphery of 3rd Pond. Using a GARMIN GPS 60 device, I recorded the start and end co-ordinates of each transect. The transect distance was measured using a 50m tape measure and the 2.5m strip either side of the transect line was measured using a 2.5 m net pole. Only trees rooted within 2.5 m either side of the transect line were sampled, and overhanging trees were not included.

Transect data were analysed by comparing the fruit loads of infected vs non infected trees. An ANOVA was used to determine whether or not there was a difference in fruit loads, as multiple variables were being compared, namely the impact of scale (if any) on fruit loads, the role of whether or not a tree was infected, and whether or not the impacts differed between transects. This was done for the data sets from Nightingale Island and Inaccessible Island to determine the impact of scale insects on the fruit loads and by comparing infected vs not infected trees along a transect. To determine the impact, if any, of scale insects on fruit load for Inaccessible and Nightingale Island I used a t-test to compare infected versus non-infected trees.

Results

Phylica *fruit loads*

There was no local variation in mean *Phylica* fruit loads between Wilkins' Bunting territories at the Ponds (12.4±6.2 fruits per branchlet) and other areas sampled (13.9±9.0, t_{22}=0.74, p=0.185). There was also no significant difference between Ponds ANOVA ($F_{1,2}$= 1.83, p= 0.14). The territory with the lowest fruit load was distant from the Ponds region, along the path approximately 500 m from the huts (7.4±3.7 fruits per branchlet) whereas the 1st Wood territories had the highest average fruit loads (15.4±9.3 fruits per branchlet).

Scale insect distribution and abundance

Scale insects on Nightingale Island are of the species *Hemiberlesia rapax*, which is different to the scale insect found on Tristan and Inaccessible Islands, *Coccus hesperidum*. Both species were identified by Mr I. M. Millar of the Agricultural Research Council. Scale insects were encountered throughout *Phylica* woodland on Nightingale Island (Figure 3.1). They were also found in all 24 Wilkins' Bunting territories sampled. Four territories had an average score of moderate infestation (2), whereas the other 20 sites had smaller numbers of scale insects. Scale insects were found on trees from the West Road to the southern end of the island in *Phylica* surrounding 3rd Pond, and areas in the eastern region of the island on High Ridge. Although widespread, the scale insect abundance was generally very low (1) and between very low (1) and less than moderate (1-2), with a total of 50.6 % of infected trees falling into these categories (Figure 3.2). The lowest incidence was for heavy infestations of scale (3), with 6 % of infected trees showing this level of infestation.

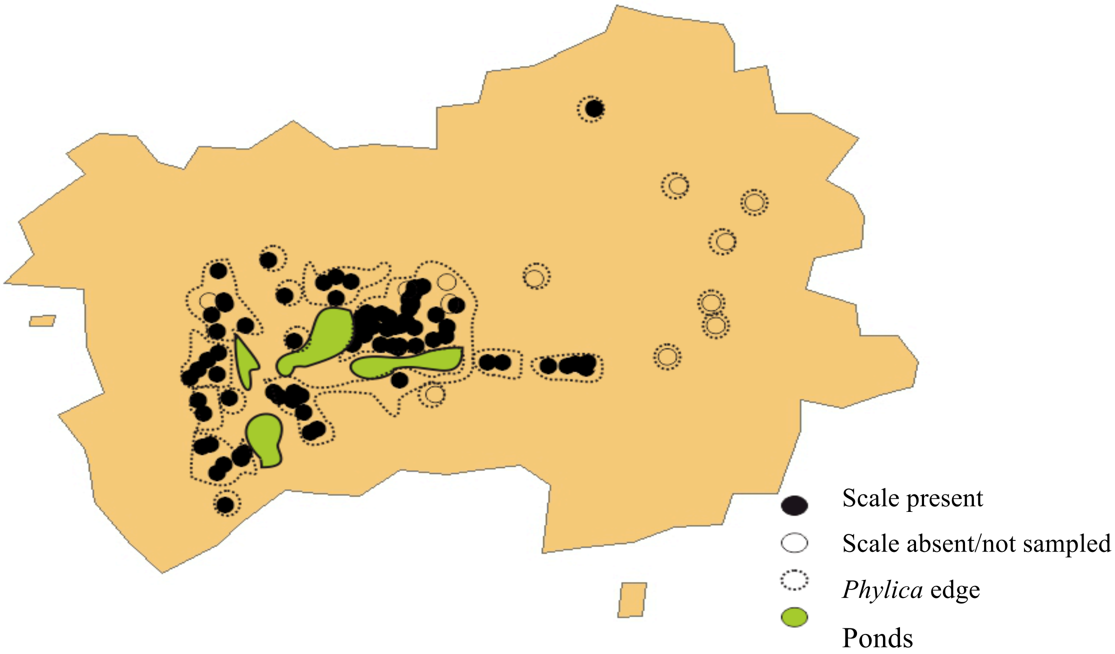

Figure 3.1: Map of the distribution (presence/absence) of the scale insect as recorded during the 2012 field season for Nightingale Island. The black circles indicate locations where scale insects were found; open circles within and near the Ponds area indicate absent scale insects whilst the open circles on the eastern side, along High Ridge, were not sampled. The dotted line shows the area of *Phylica* around the core Ponds area and also displays the isolated patches of these trees on High Ridge.

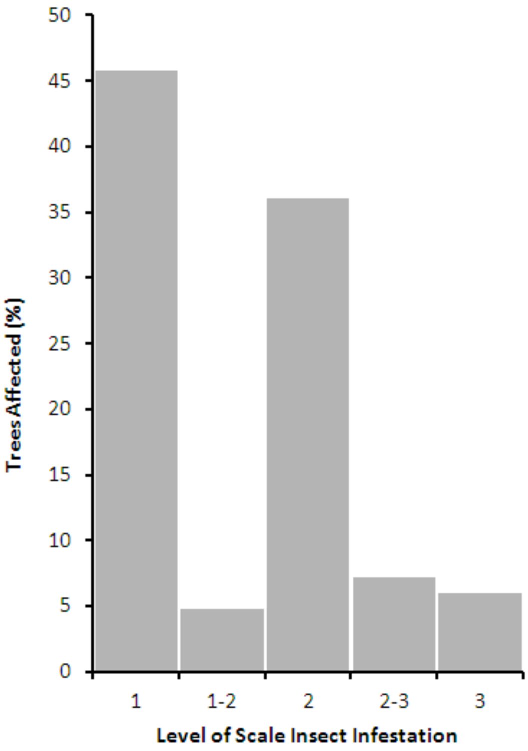

Figure 3.2: Infestation levels of scale insects on Nightingale Island, and the proportion of trees infected at different levels of scale infestation.

There was no difference in mean *Phylica* fruit load per branchlet between infected trees (12.8±6.6) and trees apparently lacking scale insects on Nightingale Island (13.4±7.4, t_{238}= 0.701, p=0.48). By comparison, at Blenden Hall on Inaccessible Island, infected trees had significantly lower fruit loads (2.6±4.3, t_{38}= 6.65, $p<0.001$) than that of uninfected trees (19.3±16.4).

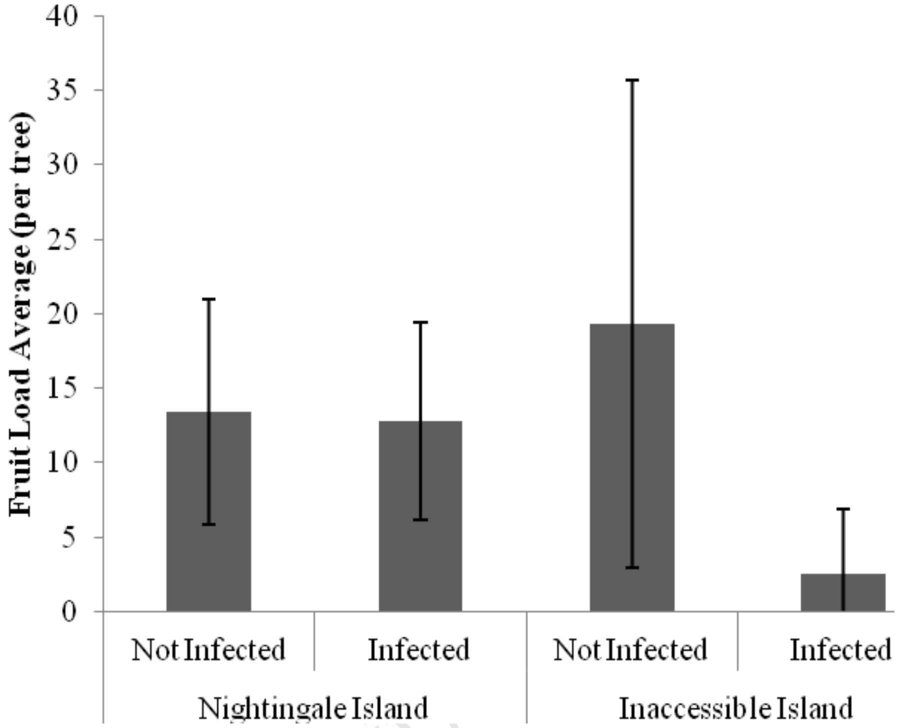

Figure 3.3: Average fruit load per tree of scale infected trees versus uninfected trees on Nightingale and Inaccessible Island. A comparison between the two islands' relative fruit loads for the areas sampled on each island. Error bars indicate 1 SD.

On the four 50 m transects on Nightingale Island, fruit loads and scale insects were scored for the 164 trees sampled. On Inaccessible Island the sample size was 332 trees along 4 different transects. For the impact of scale on *Phylica* fruit load for Nightingale Island there was no significant difference among the transects, ANOVA ($F_{4,161}$= 0.019, p=0.891). For Inaccessible Island there was also no significant difference between fruit loads along the transects due to scale infection, ANOVA ($F_{1,330}$=1.81, p=0.178).

However, when comparing infected trees of scale level 2 and 3 only (excluding scale level 1) to those trees not infected by scale on Nightingale Island, the results differ slightly. Scale still does not impact fruit load with p=0.838.

By analysing the fruit load data(including all variables) with the relevant levels of scale recorded for each territory there was no impact on the fruit load due to scale ($F_{1,3}$ =3.309, p =0.087). When comparing only the impact of scale on fruit load by disregarding the possible influence of other variables the p value does decrease ($F_{1,21}$ =3.439,p =0.078) but not sufficiently to conclude with any certainty that there is indeed an impact on fruit load by the scale insects in these territories.

The four transects show a trend in the infection rates of trees for different size classes (Figure 3.4), with a general decrease in infection from smaller to larger trees. The range of basal circumferences for the transects on Nightingale Island was 17-138 cm, with an average of 63.4 ± 23.9 cm, n= 164. The trees in the 101-120 cm size class exhibit higher infection than the preceding four size classes. However, the small sample size of the smallest (0-20cm) and largest trees (120-140cm) means that more research is needed for more robust conclusions to be drawn on the impact of scale insects across different tree size classes on Nightingale Island.

Discussion

Phylica *fruit loads*

Although it is suggested that island populations of *Phylica* such as on Nightingale Island are more likely to have within-population morphological variation (Richardson et al. 2001), and possibly therefore variation in fruit load, my results found no significant local or regional variation in fruit loads. No samples were taken around 3rd Pond, where Wilkins' Bunting territories were smallest. I expected fruit loads to be higher in the territories on the periphery of 3rd Pond because territory size and resource abundance tend to be inversely related (Marshall & Cooper 1984). However, *Phylica* fruit form in late summer and remain on the trees through winter before dehiscing the following summer, so sampling in spring reflects the abundance of fruit moderated by almost a full year of bunting predation, potentially confounding any simple link between fruit density and territory size. The average fruit load across the island was 10-15 fruits per branchlet, which is lower than the fruit load recorded for healthy trees in the lowland areas of Inaccessible Island (Figure 3.3). However, the definition of 'branchlet' is somewhat subjective, and so caution is needed when comparing data collected by different observers.

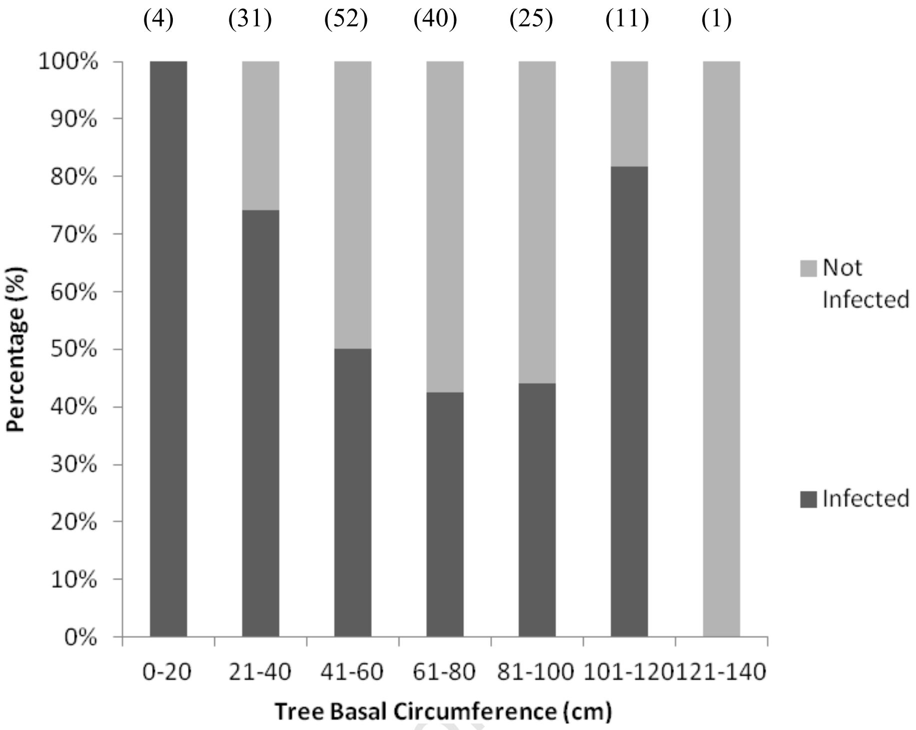

Figure 3.4: Infection rates of trees of different size classes categorised according to basal circumference. Numbers in parentheses indicate the sample size of each size class of tree.

Scale distribution and abundance

The distribution of *Hemiberlesia rapax* on Nightingale Island was more widespread than expected, considering its relatively recent discovery on the island (K. Herrian, in litt.). It is possible that the species had been overlooked for some time, but Christine Haenel collected insects on Nightingale Island in the last decade and is unlikely to have overlooked *H. rapax* if it was already well-established on the island (P.G. Ryan, pers. comm.). The fact that the species of scale insect on Nightingale Island differs from that on Tristan and Inaccessible Islands is surprising because most invasive species reaching the islands tend to arrive via Tristan.

Although widespread, the abundance of the *H. rapax* on Nightingale Island currently is low, with most localities having very few scale insects (Figure 3.2). This might be consistent with their relatively recent arrival on the island, but its wide distribution is cause for concern. Scale insects can cause canopy dieback and even the death of trees (O'Dowd et al. 2003). Increased abundance on Nightingale Island may increase the susceptibility of *Phylica* trees to fungal infection. Large parts of trees dieing greatly reduces the tree's ability to produce fruit (O'Dowd et al. 2003). On Nightingale Island the scale's low abundance could be due to the population being in the lag phase of population growth, and the abundance could still increase exponentially, making trees increasingly susceptible to fungal infections in the future. Chapter 2 illustrated the dependence of Wilkins' Bunting on *Phylica* fruit. A significant reduction in fruit load would be a major threat to the population of buntings, possibly causing declines, and would magnify genetic factors that are associated with small isolated populations.

Scale insect impacts, and associated sooty moulds, already have an impact on fruit loads on infected trees around Blenden Hall, Inaccessible Island (Figure 3.3, P.G. Ryan, unpubl. data), yet my data show no impact of scale insects on *Phylica* fruit loads on Nightingale Island (Fig 3.3). The situation on Inaccessible is exacerbated by the presence of a sooty mould (Crous et al. 2012). The marked reduction in fruit load on Inaccessible Island may be due to the combined impacts of the mould and scale insects. Although some leaf die back was observed on Nightingale Island, and was used to identify the presence of scale, the lack of sooty mould may be the reason for the limited impact on fruit load on Nightingale Island. The leaf die back presumably results from scale insects sucking the sap from the leaves. Of concern as well, is the high infection rate of smaller i.e. younger trees (Figure 3.4). High infestation and die back of young trees could result in the loss of younger trees from the population. The threat of severe storms damaging large trees would thus pose an even bigger threat to the existing *Phylica* if younger trees are being severely damaged by scale insects.

The current low abundance of *H. rapax* across Nightingale Island may account for failure to detect an impact on *Phylica* fruit loads. It would appear that the *Phylica* trees may not be as susceptible to this scale insect species. There is however a need for future research to investigate the apparent dieback recorded on certain trees. The fact that this species of scale is different to the species on Tristan and Inaccessible islands highlights the need for vigilance and stricter controls to try to prevent further introductions to Nightingale Island. This is especially true for preventing sooty mould transfer from Inaccessible to Nightingale Island in the future. The practice of boot cleaning may need to be supplemented with other measures such as prohibiting direct movement between Nightingale and Inaccessible Island in order to ensure Nightingale Island remains sooty mould free.

Chapter 4. Notes on the breeding behaviour of Wilkins' Bunting

Introduction

Very little is known about the breeding biology of the *Nesospiza* buntings on Nightingale Island (Collar & Stuart 1985, Fraser & Briggs 1992). The most extensive work has been done on Inaccessible Island buntings during the summer months of 1989-1990 and 1999-2000 (Ryan & Moloney 2002). Published information on the nests of the buntings on Nightingale Island is restricted to some observations by Hagen (1952) and Elliot (1957) of three Nightingale Bunting and five Wilkins' Bunting nests. Wilkins' Bunting lays 1-2 eggs in an open cup nest with breeding occurring between November and January (Ryan et al. 2007). The only record for a Nightingale Bunting nest reported a clutch size of 4 eggs (Hagen 1952), but this is almost certainly an error (Elliot 1957); they probably also lay 1-2 eggs (Ryan 2007) and are believed to breed slightly earlier than Wilkins' Buntings, from October to January, based on observations by Richardson (1984) of fledged young in late November of 1973. However, subsequent visits did not find breeding behaviour even toward late November (Ryan pers. obs. 1989). Both species are thought to be territorial at least for part of the year from September to March (Ryan 2007).

By comparison, the breeding biology of the Inaccessible Bunting *Nesospiza acunhae* is much better understood as a result of more extensive studies of this species complex (Fraser & Briggs 1992, Ryan 1992, Ryan 2001, Ryan & Moloney 2002, Ryan et al 2007, Ryan 2008). A clutch size of between 1-2 (1.8) eggs is the norm with an incubation period of 17-18 days by the female only (Ryan & Moloney 2002). During incubation the female is fed by the male near the nest. The nestling period is 18-21 days, with the young birds remaining in dense cover for at least a further ten days before accompanying the adults during foraging (Ryan & Moloney 2002). Only a single brood is reared per season (Ryan & Moloney 2002, Ryan 2007). In tussock grassland on the coast of Inaccessible Island, the large billed *N. a. dunnei* breed slightly earlier and exhibit lower fledging success but higher post fledging survival then the small-billed *N. a. acunhae* (Ryan & Moloney 2002).

It is important to collect comparative information on the breeding biology of the two bunting species that occur on Nightingale Island. Data on Wilkins' Bunting are especially valuable, given the small population size and endangered status of this species. In this short chapter I report the behaviour of Wilkins' Bunting during the early breeding season. Unfortunately I was forced to leave the island before any eggs had hatched, but I could infer laying dates assuming their incubation period is similar to that of Inaccessible Buntings.

Materials and Methods

Breeding biology information

Observations on the breeding biology of buntings on Nightingale Island were made from 14 September to 26 November 2012. Nests were located by observing marked pairs that spent long periods in a restricted area of the territory. However, most nests were located by the female's begging behaviour when fed by the male during incubation. All behaviour associated with nest building, incubation, nest parameters and egg measurements were recorded and the GPS co-ordinates of each nest site also noted. Notes on nest building were taken by observing females that were located whilst constructing nests.

Most nests were measured, recording the height above ground (cm), and the inner diameter and depth of the nest cup (cm). Eggs of one nest (SW of 1st Pond) were not measured due to the difficulty of accessing the nests' locality and two nests did not contain eggs at the time of departure from the island. Notes were made on the surrounding vegetation and the materials used in the construction of the nests. Final clutch size was determined by visiting the nest at least twice, with an interval of 3 days between visits. Disturbance, especially during nest building and early incubation, was kept to a minimum by visiting the nest area no more than once every day. Observations of nest visitation and construction typically were made from a distance of >10 m to minimise the impact on the behaviour of the birds.

For each of the nests, except in one case where it was impossible to measure the eggs due to the nest location, the egg width and length was measured to the nearest 0.1 mm, using Vernier callipers. An elongation index was calculated as egg length/width (Ryan & Moloney 2002). To minimise disturbance, the eggs were measured when the female flew off the nest, either to be fed by the male or to feed in *Phylica* trees. To determine if any predation of eggs had taken place the nests were checked once every three days and all nests were checked on the final day of the field season (26 November 2012).

Results and Discussion

Aggressive territorial interactions of Wilkins' Buntings intensified from mid-October 2012 when males become increasingly vocal and there were increasing numbers of interactions between neighbouring pairs. Singing by males was sporadic and largely confined to the morning from mid-September to early October, but became more sustained, occurring all day by the end of October. Nightingale Buntings showed increased territorial interactions from early November**.** An interesting observation was that of the lack of Nightingale Bunting nests that were found. This may suggest that breeding commences later than the month of October, which currently is thought to be the beginning of the breeding season, and is similar to the pattern on Inaccessible where the larger billed birds begin breeding a few weeks earlier than the smaller billed birds (Ryan & Moloney 2002).

Nest building by Wilkins' Buntings was first observed on 26 October, when two different females were observed breaking off twigs from *Phylica* trees and collecting bunches of short pieces of tussock grass. Although birds had often been observed to bite *Phylica* twigs and tussock stems, this was the first occasion they carried a number of pieces of vegetation. These initial observations resulted in the females dropping the pieces of material and subsequent visits to the areas in the following days did not yield any further similar behaviour.

Nest building was observed in two cases, when the female was observed carrying material into the same area on a number of occasions over several days. I recorded the construction of these two nests and the male visitation to the nest at five nests. The duration of observation, for nest construction and visits to nests, was a total of 10 hrs and 23 minutes. The female of the pair at the entrance to 1st wood was seen nest building on 1 November, and was observed constructing every day until 6 November, then again on 12 November after a period of inclement weather with heavy rain that may have interrupted nest building. She was first seen sitting on her nest on 16 November 2012, and an egg was observed on 17 November. Nest building thus takes at least 5 days.

The first nest was discovered on the 14th November at the northern edge woodland of 3rd Pond. A single egg had already been laid, but no further eggs were laid, so the clutch was apparently complete when found. However the egg had not hatched by 26 November, so assuming an incubation period of 17-18 days (Ryan & Moloney 2002), the earliest laying date was 10 November.

Nest building was carried out by the female only. While she constructed the nest, the male often perched nearby, calling vociferously. Territorial interactions with neighbouring pairs still involved both birds, even once the female had begun incubation. The female would fly off the nest to defend the territory from possible intruders. To feed the female, the male would fly toward the nest calling and the female would initially respond by calling from the nest, then appear from the nest and begin to beg for food with a buzzing call and wings quivering. Once fed, the female would either continue to feed nearby or return to the nest. The longest time of absence from the nest was 12 min (4.84 ±2.81 min, n=19). Males mostly fed their partner every 10-20 min (15.83 ±4.40 min, n=6) but in one case no feeding was observed for 62 min (excluded from analysis as an outlier). As a result of this the female left the nest to feed in the *Phylica* trees rather than wait for the returning male. Fraser & Briggs (1992) observed two incubating female Inaccessible Buntings for 11.7 h and 32.5 h, respectively. The times of absence from the nests ranged from 0.2 – 67.2 min (6.5 ± 13.0 min, n=27) and 0.1 – 17.2 min (3.6 ± 3.4 min, n=77). The mean values for absence are similar to those of Wilkins' Buntings. The visits by males were recorded by Fraser & Briggs (1992) as a daily feeding rate of number of visits per hour. For the same two nests the feeding rates were 1.9 – 6.2 per hour (2.8 ± 1.7, n=6) and 1.0 – 3.0 per hour (2.7 ± 0.8, n=10). The mean values relate to a visit every 21.4 and 22.2 min respectively. The initial data recorded for feeding rate on Nightingale Island are similar to these observations.

Both sexes were observed to defend the nest and general area from Tristan Thrushes (*Nesocichla emerita procax*) by harassing and chasing them far away from the nest. It would be plausible to suggest that the thrushes pose the greatest threat as predators to the eggs and chicks.

Location of nests and nest measurements

In total, ten nests were found; two on the northern edge of 3rd Pond, two on the eastern side of 1st Pond, two on the northern edge of 2nd, one between 1st and 2nd Ponds, and the remaining nests were scattered through 1st Wood. Nine nests were located in the base of a large tussock; the exception at the northern end of 2nd Pond was constructed in a large clump of the fern *Asplenium obtusatum* away from tussock grassland or *Phylica* trees. None of the nests were constructed on the ground. The height above the ground varied from 25-110 cm (54±28 cm, n=10). This range is not dissimilar to Inaccessible Buntings, which have been recorded to nest up to 1.2 m above ground, although all nests of large-billed birds have been within 20 cm of the ground (Ryan & Moloney 2002).

The nests were built from *Spartina* leaves, *Phylica* twigs and small branches, and some contained leaves of the sedge *Carex insularis*. The nest that was constructed in the *Asplenium* fern was built entirely from dead leaves of *Carex insularis*. All the other nests were built from more than one type of material. Nest cups ranged from 7-9 cm across (8.1±0.8 cm, n=8) and 6-10 cm deep (7.5±1.7 cm, n=8).

Clutch size and egg dimensions

Based on the small sample size of 7 completed clutches (one nest's first egg was laid the day prior to departure and therefore final clutch size was unknown), Wilkins' Bunting has a clutch size of 1-2 eggs, the same as the Inaccessible *Nesospiza* buntings, with an average in this sample of 1.57. Ten eggs from 7 nests were measured: average length was 27.3±0.55 mm (range 26.5-28.4) and width 19.1±0.14 mm (18.8-19.3 mm). The elongation index ranged from 1.398-1.472 (1.429±0.023).

Conclusions

All of the described behaviour of Wilkins' Buntings on Nightingale Island, from nest building to incubation by the female only, is consistent with the behaviour exhibited by the better known Inaccessible Bunting complex (Fraser & Briggs 1992, Ryan & Moloney 2002). Although limited to a small sample size, the visitation rate and absence from nests by females is in agreement with observations on Inaccessible

Island by Fraser & Briggs (1992). A notable difference is the building of nests above the ground by Wilkins' Bunting whereas the large billed birds on Inaccessible construct their nests on the ground (Ryan & Moloney 2002).

From this research, the onset of breeding is mid to late November for Wilkins' Buntings. Previous observations during October 1989 and 2007 found no evidence of breeding, and none of the birds caught had brood patches evident (P.G. Ryan, unpubl. data). A day visit in late November 1989 found a single gravid female Nightingale Bunting, and a female Wilkins' Bunting with a vascularised brood patch, suggesting that breeding was taking place (P.G. Ryan, unpubl. data). These observations show some evidence for breeding commencing in late November.

Although no nests for Nightingale Buntings were found, birds were observed carrying nesting material from mid November. Birds carrying nesting material and gravid females were caught in early December 2009 (P.G. Ryan, unpubl. data.), suggesting that they breed later than the Wilkins' Buntings, which is the same pattern as on Inaccessible, where large billed birds breed a few weeks earlier than the small billed birds (Ryan & Moloney 2002). Future research should prioritise finding and recording nests of Nightingale Buntings, and incorporate breeding success and fledging survival to supplement this initial research on the breeding biology of the *Nesospiza* on Nightingale Island.

Chapter 5. Synthesis: Key findings and future research priorities for conservation of the Wilkins' Buntings

Key findings

Population estimation

The reassessment of the population of Wilkins' Bunting on Nightingale Island was the main objective of this project. I established that previous estimates of 50 breeding pairs are conservative. In the main study area, at least 56 different pairs had one or more birds individually colour banded. In the 'Ponds' area there were at least 10 other pairs that remained unringed, I observed 3 unringed pairs in the 1st Wood area, and based on limited observations estimated a further 8-10 pairs on High Ridge. The estimated number of pairs of Wilkins' Buntings is thus 80 (75-85) pairs based on current knowledge, and a large degree of uncertainty around the figure for High Ridge due to the poor coverage of the scattered *Phylica* trees there. The remaining areas on the island, where bunting numbers are uncertain, are very steep, inaccessible slopes with scattered *Phylica* patches. Based on large-billed birds on Inaccessible Island occupying similar habitat, one should find Wilkins' Buntings in these areas, and future searches will be vital in determining numbers of buntings here.

It is concerning that even with a larger number of breeding pairs present, the total population estimate is not much higher than the 200 individuals estimated by Ryan (2008). Following this field season the population estimate is at least 216 birds but probably not more than 250 birds. Of further concern is the small proportion of immature birds caught (25%, n=114). This may suggest low breeding success or point to the possibility that not all of the pairs of Wilkins' Buntings are breeding. However, two considerations need to be made concerning whether or not low numbers of immatures does support either suggestion. Firstly, one needs to determine whether or not a bias toward catching territorial birds results in fewer immatures being caught. Secondly, to determine what the survival rate is, as a relatively high survival rate would result in a low proportion of immatures. However, the presence of 2nd year birds would suggest that the number of immatures is lower than expected for a population of approximately 80 breeding pairs. Of interest was the presence of two different immatures in September that were still associated with their presumed parents. These two immatures were not observed with the parent birds from mid-October and were resighted subsequently on their own, having left the parent birds.

Territory sizes and breeding pair densities

Wilkins' Bunting territories ranged in area from 0.012 ha to 0.34 ha, with the 3rd Pond area having significantly smaller territories based on recorded observations. It is important to consider that following the birds in the steeper areas surrounding 3rd Pond is difficult and may have lead to contributing to smaller mapped territories. The smaller territories in this area appear to be largely due to the small patches of *Phylica* around this Pond.

The overall density of the 55 pairs for which territories were mapped was 7.24 pairs.ha^{-1} (Range 5.72 pairs.ha^{-1}- 15.28 pairs.ha^{-1}). Based on previous estimates one would expect a mean density of 10 pairs.ha^{-1}. The current maximum population estimate of 250 birds and approximately 10 ha of *Phylica* present gives 25 birds per hectare, but Wilkins' Buntings are not restricted to *Phylica* woodland only, as seen by numerous observations within *Spartina* grassland.

Foraging ecology and diet

The preferred foraging areas of adults Wilkins' Buntings differed markedly from those used by immature birds. *Phylica* trees were the favoured habitat for adult birds whilst the immatures foraged mainly on the ground under fern-bush. This difference may result from immatures avoiding harassment by territorial adults during the start of the breeding season. The low incidence of observing immature Wilkins' Buntings in *Spartina* may have been due to the denseness of this vegetation, and the unobtrusive behaviour of immatures compared to territorial adults. A future research priority would be to assess whether this habitat difference persists year round. Even whilst foraging on the ground, immature Wilkins' Buntings showed a preference for fallen *Phylica* seeds, although they also gleaned invertebrates from lichen, moss and *Spartina*. By comparison, the smaller Nightingale Bunting was observed to feed mostly on smaller seeds and to glean invertebrates from various plant species.

Invasive scale insects and Phylica *fruit loads*

The density of *Phylica* fruits was similar in 24 Wilkins' Bunting territories. The average fruit load across the island was 10-15 fruit per terminal branchlet. Unlike on Inaccessible Island, where the scale insect *Coccus hesperidum* and associated fungal infections reduce fruit loads, the introduced scale insect *Hemiberlesia rapax* (Comstock), currently appears to have limited effect on fruit loads on Nightingale Island. The scale insect was more widespread than previously known, but generally occurred at low levels of abundance. I found no sign of any fungal infection on Nightingale Island by the sooty mould associated with scale insects on Inaccessible Island.

Future conservation management recommendations

Of vital importance is the continued monitoring of the colour banded birds and the capture and ringing of more birds, especially juveniles to estimate survival rates for different ages and sexes of Wilkins' Buntings. It is planned that staff from Tristan's Conservation Department will continue this work. Other parameters that could be investigated in future, now that birds have been individually colour banded, are to confirm whether birds keep the same partners and territories from year to year. Of particular interest is to determine winter distribution and behaviour, to assess whether birds remain within their territories year round. Currently we only know that both bunting species are territorial from September to March, based mainly on observations from Inaccessible Island.

The initial objective of the 2012 project was to stay on Nightingale Island through the breeding season until mid-January but this was not possible due to logistical reasons. This meant that no data on incubation period, time until fledging, breeding success, and post fledging survival could be collected. A further priority would be to find Nightingale Bunting nests to record their clutch size and other aspects of their breeding biology. For these reasons it would be ideal for another, later field season to record these aspects of the breeding biology in order to gain a more holistic understanding of these two species on Nightingale Island.

Scale insect impacts on Phylica *trees*

Future studies continuing from this initial work should be done to determine if the abundance and distribution of the scale insect is increasing. Repeated transects in the same areas where the current transects were done are needed to compare scale insect impacts over several years. Fixed point photography might provide a useful tool to monitor long term trends in the extent of *Phylica* woodland, and to detect local die back potentially resulting from scale insect infestations.

Concluding remarks

This study has provided baseline information for further studies that will hopefully contribute to better understanding of the *Nesospiza* buntings of the Tristan archipelago, and more specifically help in successfully conserving the endangered, single island endemic Wilkins' Bunting. Based on this study it will remain as an Endangered species on the IUCN Red list. There remains plenty of scope for future research and studies, especially on the breeding biology of *Nesospiza* on Nightingale Island, as many questions remain unanswered. We have only just begun to better understand these unique birds and further research should be prioritised on Nightingale Island. With increased knowledge of the birds on Nightingale Island, and further work on Inaccessible Island, we will be able to piece together the fascinating story of these unique songbirds in this remote part of the world.

References

Abbott, I., L. K. Abbott, and P. R Grant. 1977. Comparative ecology of Galapagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. Ecological Monographs **47**:151-184.

Abbott, I. 1978. The significance of morphological variation in the finch species on Gough, Inaccessible and Nightingale Islands, South Atlantic Ocean. Journal of Zoology, London. **184**:119-125.

Anten, N. P. R., and D. D. Ackerly. 2001. Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. Functional Ecology **1**:252-262.

Altizer, S., J. Foufopoulos, and A. Gager. 2001. Conservation and diseases. Pages 109-126 in S. Levin, editor. *Encyclopedia of Biodiversity*. Academic Press, San Diego.

Baker., P. E., G. Gass, P. G. Harris, and R. W. le Maitre. 1964. The volcanological report of the Royal Society Expedition to Tristan da Cunha, 1962. Philosophical Transactions of the Royal Society, Series A **256**:439-578.

Benning, T. L., D. LaPointe, C. T. Atkinson, and P. M. Vitousek. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modelling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences **99**:14246–14249.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Biber, E. 2002. Patterns of endemic extinctions among island bird species. Ecography **25**:661-676.

BirdLife International. 2008. Threatened Birds of the World 2008. B. International, Cambridge, UK.

Blackburn, T. M., O. L. Petchey, P. Cassey, and K. J. Gaston. 2005. Functional diversity of mammalian predators and extinction in island birds. Ecology **86**:2916-2923.

Both, C., and M. E. Visser. 2003. Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. American Naturalist **161**:326–336.

Brook, B. W., and J. L. Kikkawa.1998. Examining threats faced by island birds: a population viability analysis on the Capricorn Silvereye using long-term data. Journal of Applied Ecology **35**:491-503.

Carlquist, S. 1965. *Island Life: The Natural History of the Islands of the World.* Natural History Press, New York, United States.

Carlquist, S. 1966a. The biota of long-distance dispersal. I. Principles of dispersal and evolution. Quarterly Reviews in Biology **41**:247-270.

Carlquist, S. 1966b. The biota of long-distance dispersal. II. Loss of dispersability in the Pacific Compositae. Evolution **20**:30-48.

Case, T. J., D. T. Bolger, and A. D. Richman. 1992. Reptilian Extinctions: The Last Ten Thousand Years. Pages 90-125 in P. L. Fiedler, and S. K. Jain, editors. *Conservation Biology: the Theory and Practice of Nature Conservation, Preservation and Management*. Chapman and Hall, New York.

Clavero, M., L. Brotons, P. Pons, and D. Sol. 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation **142**:2043–2049.

Cody, M. L., and J. M. Overton. 1996. Short-term evolution of reduced dispersal in island plant populations. Journal of Ecology **84**:53-61.

Collar, N.J., and S. N. Stuart. 1985. *Threatened Birds of Africa and Related Islands*. The ICBP/IUCN Red Data Book, Part I, 3rd edition. International Council for Bird Preservation and International Union for Conservation of Nature and Natural Resources. Cambridge, UK.

Cowie, R. H., and B. S. Holland. 2008. Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. Philosophical Transactions of the Royal Society, Series B **363**:3363–3376.

Crous, P.W., J. Z. Groenewald, P. G. Ryan, and M. J. Wingfield. 2012. Fungal Planet description sheet 147: *Seiridium phylicae*. Persoonia **29**:186-187.

Cuthbert, R. J., and G. M. Hilton. 2004. Introduced house mice *Mus musculus*: a significant predator of endangered and endemic birds on Gough Island, South Atlantic Ocean? Biological Conservation **117**:483–489.

Dean, W. R. J., S. J. Milton, P. G. Ryan, and C. L. Moloney. 1994. The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale Islands in the South Atlantic Ocean. Vegetatio **113**:13-23.

de Beer, S. J., G. M. Lockwood, J. H. F. A. Raijmakers, W. A. Scott, H. D. Oschadleus, and L. G. Underhill. (eds). 2001. SAFRING bird ringing manual. ADU guide 5. Avian Demography Unit, University of Cape Town, Cape Town.

de Lima, R. F., J. P. Bird, and J. Barlow. 2011. Research effort allocation and the conservation of restricted-range island bird species. Biological Conservation **144**:627-632.

Delport, W., Grant, T. J, Ryan, P. G, and P. Bloomer. 2006. Ten microsatellite loci for evolutionary research on *Nesospiza* buntings. Molecular Ecology Notes **6**:1180-1183.

Diamond, J. M. 1984a. "Normal" extinctions of isolated populations. Pages 191-245 in H. M. Nitecki, editor. *Extinctions*. University of Chicago Press, Chicago.

Diamond, J. M. 1984b. Historic extinctions: a Rosetta stone for understanding prehistoric extinctions. Pages 824-862 in P. S. Martin and R. G. Klein, editors. *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, Arizona.

Diamond, J. M., K. D. Bishop, and S. van Balen. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation Biology **1**:132-142.

Diamond, J. 1989. The present, past and future of human caused extinctions. Philosophical Transactions of the Royal Society of London, Series B **325**:469–476.

Dobson, A.P., and R. Carper. 1992. Global warming and potential changes in host-parasite and disease-vector relationships. Pages 201-217 in R. L. Peters, and T. E. Lovejoy, editors. *Global Warming and Biological Diversity*. Yale University Press, London.

Dobson, A. P., and J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. Philosophical Transaction of the Royal Society of London, Series B **356**:1001-1012.

Duncan, R. P., and T. M. Blackburn. 2004. Extinction and endemism in the New Zealand avifauna. Global Ecology and Biogeography **13**:509–517.

Duncan, R. P., and T. M. Blackburn. 2007. Causes of extinctions in island birds. Animal Conservation **10**:149-150.

Elliott, H. F. I. 1957. A contribution to the ornithology of the Tristan da Cunha group. Ibis **99**:545-586.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology **10**:1500-1508.

Frankham, R. 1998. Inbreeding and extinction: island populations. Conservation Biology **12**:665–675.

Fraser, M.W., and D. J. Briggs. 1992. New information on the *Nesospiza* buntings at Inaccessible Island, Tristan da Cunha, and notes on their conservation. Bulletin of the British Ornithologists' Club **112**:191-205.

Fraser, M. W., W. R. J. Dean, and J. C. Best. 1992. Observations on the Inaccessible Island rail *Atlantisia rogersi*: the world’s smallest flightless bird. Bulletin of the British Ornithologists Club **112**:12-22.

Fraser, M. W., P. G. Ryan, W. R. J. Dean, D. J. Briggs, and C. L. Moloney. 1994. Biology of the Tristan thrush *Nesocichla eremita*. Ostrich **65**:14-25.

Fretwell, S. D., and H. J. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**:16–36.

Fritts, T. H., and G. H. Rodda 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecology, Evolution, and Systematics **29**:113–40.

Fuller, E. 1987. *Extinct Birds*. Viking/Rainbird, London.

Gaston, K. J. 2002. Extinction. Pages 344–349 in M. Pagel, editor. *Encyclopedia of Evolution*. Volume 1. Oxford University Press, New York.

Gaston, K. J., and T. M. Blackburn. 1995. Birds, body size and the threat of extinction. Philosophical Transactions of the Royal Society, Series B **347**:205–212.

Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. Journal of Applied Ecology **46**:1–9.

Gehring, C. A., N. S. Cobb, and T. G. Whitham. 1997. Three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines. American Naturalist **149**:824-841.

Gillespie, R. G., E. M. Claridge, and G. K. Roderick. 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Molecular Ecology **17**, 45–57.

Grant, P. R. 1999. *Ecology and Evolution of Darwin's Finches: (With a new preface and afterward)*. Princeton University Press, Princeton.

Grant, T. J. 2004. Molecular evolution and population genetics of the *Nesospiza* buntings. MSc thesis, University of Pretoria.

Grant, B. R., and P. R. Grant. 1996. High survival of Darwin's finch hybrids: effects of beak morphology and diets. Ecology **77**:500-509.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science **296**:707-711.

Grant, P. R., B. R. Grant, J. N. M. Smith, I. J. Abbott, and L. K. Abbott. 1976. Darwin's finches: population variation and natural selection. Proceedings of the National Academy of Sciences of the USA **73**:257-261.

Groombridge, B. 1992. *Global Biodiversity - Status of the Earth's Living Resources: A Report Compiled by the World Conservation Monitoring Centre*. Chapman and Hall, London.

Hagen, Y. 1952. Birds of Tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937-1938 **20**:1-248.

Halliday, T. 1978. *Vanishing Birds: their Natural History and Conservation*. Sedgewick & Jackson, London.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science **296**:2158–2162.

Hockey, P. A. R., R. M. Wanless, and R. von Brandis. 2011. Demographic resilience of territorial island birds to extinction: the flightless Aldabra Rail *Dryolimnas* (*cuvieri*) *aldabranus* as an example. Ostrich **82**:1-9.

Holdaway, R. N., T. H. Worthy, and A. J. D. Tennyson. 2001. A working list of breeding bird species of the New Zealand region at first human contact. New Zealand Journal of Zoology **28**:119–187.

Holdgate, M. W. 1967. The influence of introduced species on the ecosystems of temperate oceanic islands. International Union for Conservation of Nature and Natural Resources Publication **9**:151-176.

Houston, D. R., and H. T. Valentine. 1988. Beech bark disease: the temporal pattern of cankering in aftermath forests of Maine. Canadian Journal of Forest Research **18**:38-42.

Hughes, L., and M. Westoby. 1994. Climate change and conservation policies in Australia: coping with change that is far away and not yet certain. Pacific Conservation Biology **1**:308-318.

IUCN. 2008. *IUCN Red List of Threatened Species*. International Union for Conservation of Nature, Gland.

James, H. F., T. W. Stafford Jr, D. W. Steadman, S. L. Olson, P. S. Martin, A. J. Jull, and P. C. McCoy. 1987. Radiocarbon dates on bones of extinct birds from Hawaii. Proceedings of the National Academy of Sciences of the USA **84**:2350-2354.

Jansen van Rensburg, A., P. Bloomer, P. G. Ryan, and B. Hansson. 2012. Ancestral polymorphism at the major histocompatibility complex (MHCIIbeta) in the *Nesospiza* bunting species complex and its sister species (*Rowettia goughensis*). BMC Evolutionary Biology **12**:143-155.

Johnson, T. H, and A. J. Stattersfield. 1990. A global review of island endemic birds. Ibis **132**:167-180.

Lack, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge, UK.

Lack, D. 1971. *Ecological Isolation in Birds*. Blackwell Publishing, Oxford, UK.

Lowe, P. R. 1923. Notes on some land birds of the Tristan da Cunha group collected by the Quest Expedition. Ibis **5**:511-529.

Manne, L. L., T. M. Brooks, and S. L. Pimm. 1999. Relative risk of extinction of passerine birds on continents and islands. Nature **399**:258-261.

Marshall, M. R., and R. J. Cooper. 2004 Territory size of a migratory songbird in response to caterpillar density and foliage structure. Ecology **85**:432–445.

Milberg, P., and T. Tyrberg. 1993. Naive birds and noble savages—a review of man-caused prehistoric extinctions of island birds. Ecography **16**:229-250.

Moors, P. J., I. A. E. Atkinson, and G. H. Sherley. 1992. Reducing the rat threat to island birds. Bird Conservation International **2**: 93–114.

Morrison, S. A., T. S. Sillett, C. K. Ghalambor, J. W. Fitzpatrick, D. M. Graber, V. J. Bakker, R. Bowman, C. T. Collins, P. W. Collins, K. S. Delaney, D. F. Doak, W. D. Koenig, L. Laughrin, A. L. Lieberman, J. M. Marzluff, M. D. Reynolds, J. M. Scott, J. N. Vickers, and W. M. Boyce. 2012. Proactive conservation management of an island-endemic bird species in the face of global change. BioScience **6**:1013-1021.

Moseley, H. N. 1892. *Notes by a naturalist, being an account of various observations made during the voyage of H.M.S.* Challenger *round the world in the years 1872-1876*. Macmillan, London.

Mountfort, G. 1988. *Rare Birds of the World*. Collins, London.

Newton, I. 2003. *Speciation and Biogeography of Birds*. Academic Press, London.

O'Dowd, D. J., P. T. Green, and P. S. Lake. 2003. Invasional meltdown on an oceanic island. Ecology Letters **6**:812–817.

Oleksyn, J., P. Karolewski, M. J. Giertych, R. Zytkowiak, P. B. Reich and M. G. Tjoelker. 1998. Primary and secondary host plants differ in leaf-level photosynthetic response to herbivory: evidence from *Alnus* and *Betula* grazed by the Alder Beetle, *Agelastica alni*. New Phytologist **140**:239-249.

Olson, S. L., and H. F. James. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. Science **217**:633-635.

Phillimore, A. B., I. P. F. Owens, R. A. Black, J. Chittock, T. Burke, and S. M. Clegg. 2008. Complex patterns of genetic and phenotypic divergence in an island bird and the consequences for delimiting conservation units. Molecular Ecology **17**:2839-2853.

Pimm, S. L. 1987. The snake that ate Guam. Trends in Ecology and Evolution **2**:293-295.

Pimm, S. L., M. P. Moulton, and L. J. Justice. 1994. Bird extinctions in the central Pacific. Philosophical Transactions of the Royal Society, Series B **344**:27-33.

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. Nature **409**:185-188.

Raikow, R. J. 1976. The origin and evolution of the Hawaiian honeycreepers (Drepanididae). Living Bird **15**:95-117.

Rand, A L 1955. The origin of landbirds of Tristan da Cunha, Nightingale and Inaccessible Islands. Fieldiana Zoology **37**:139-166.

Reid, W. V., and K. R. Miller. 1989. *Keeping Options Alive: The Scientific Basis for Conserving Biodiversity*. World Resources Institute, Washington, D.C.

Retuerto, R., B. Fernanez-Lema, R. Roiloa, and J. R. Obeso. 2004. Increased photosynthetic performance in holly trees infested by scale insects. Functional Ecology **18**:664-669.

Richardson, J. E., F. M. Weitz, M. F. Fay, Q. C. B. Cronk, H. P. Linder, G. Reeves, and M. W. Chase. 2001. Phylogenetic analysis of *Phylica* L. (Rhamnaceae) with an emphasis on island species: evidence from plastid trnL-F and nuclear internal transcribed spacer (ribosomal) DNA sequences. Taxon **50**:405-427.

Richardson, J. E., M. F. Fay, Q. C. B. Cronk, and M. W. Chase. 2003. Species delimitation and the origin of populations in island representatives of *Phylica*. Evolution **57**:816-827.

Richardson, M. E. 1984. Aspects of the ornithology of the Tristan da Cunha group and Gough Island, 1972-1974. Cormorant **12**:122-201.

Rodgers, A.R., and A. P. Carr. 1998. *HRE: The Home Range Extension for ArcView*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Roux, J. P., P. G. Ryan, S. J. Milton, and C. L. Moloney. 1992. The vegetation of Inaccessible Island, central South Atlantic Ocean, with notes on Nightingale Island. Bothalia **22**:93-109.

RStudio. 2012. RStudio: *Integrated development environment for R* (Version 0.96.122). Boston, MA. Retrieved December 20, 2012. Available from http://www.rstudio.org/.

Ryan, P.G. 1992. The ecology and evolution of *Nesospiza* buntings. Ph.D. thesis, University of Cape Town, South Africa.

Ryan, P. G. 2001. Morphological heritability in a hybrid bunting complex: *Nesospiza* at Inaccessible Island. Condor **103**:429-438.

Ryan P. G. editor 2007. *Field Guide to the Animals and Plants of Tristan da Cunha and Gough Island*. Pisces Publications, Newbury.

Ryan, P. G. 2008. Taxonomic and conservation implications of ecological speciation in *Nesospiza* buntings on Tristan da Cunha. Bird Conservation International **18**:20–29.

Ryan, P. G., P. Bloomer, C. L. Moloney, T. Grant, and W. Delport. 2007. Adaptive speciation in South Atlantic island finches. Science **315**:1420–1423.

Ryan, P. G., and C. L. Moloney. 1991. Tristan Thrushes kill adult White-bellied Storm-petrels. Wilson Bulletin **103**:130-132.

Ryan, P. G., and C. L. Moloney. 2002. Breeding behaviour, clutch size and egg dimensions of *Nesospiza* buntings at Inaccessible Island. Ostrich **73**:52-58.

Ryan, P. G., Moloney, C. L, and J. Hudon. 1994. Colour variation and hybridization among *Nesospiza* buntings on Inaccessible Island, Tristan da Cunha. Auk **111**:314-327.

Ryan, P.G., and R. A. Ronconi. 2010. The Tristan Thrush *Nesocichla eremita* as seabird predator. Ardea **98**:247-250.

Ryan, P. G., B. P. Watkins, and W. R. Siegfried. 1989. Morphometrics, metabolic rate and body temperature of the smallest flightless bird: the Inaccessible Island rail. Condor **91**:465-467.

Savidge, J. A. 1987. Extinction of an island avifauna by an introduced snake. Ecology **68**:660-668.

Schneider, S. H., L. Mearns, and P. H. Gleick. 1992. Climate- change scenarios for impact assessment. Pages 38-55 in R. L. Peters and T. E. Lovejoy, editors. *Global Warming and Biological Diversity*. Yale University Press, London.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology **50**:278-296.

Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. Ecology **57**:629-648.

Thibault, J. C., J-L. Martin, A. Penloup, and J-Y. Meyer. 2002. Understanding the decline and extinction of monarchs (Aves) in Polynesian islands. Biological Conservation **108**:161–174.

Thomson, V. P., S. A. Cunningham, M. C. Ball, and A. B. Nicotra. 2003. Compensation for herbivory by *Cucumis sativus* through increased photosynthetic capacity and efficiency. Oecologia **134**:167-175.

Trevino, H. S., A. L. Skibial, T. J. Karels, and F. S. Dobson. 2007. Threats to avifauna on oceanic islands. Conservation Biology **21**:125–132.

van der Meij, M. A. A., and R. G. Bout. 2004. Scaling of jaw muscle size and maximal bite force in finches. Journal of Experimental Biology **207**:2745-2753.

van der Meij, M. A. A., and R. G. Bout. 2006. Seed husking time and maximal bite force in finches. Journal of Experimental Biology **209**:3329-3335.

Walsh, J. C., O. Venter, J. E. M. Watson, R. A. Fuller, T. M. Blackburn, and H. P. Possingham. 2012. Exotic species richness and native species endemism increase the impact of exotic species on islands. Global Ecology and Biogeography **21**:841–850

Wace, N. M., and J. H. Dickson. 1965. The terrestrial botany of the Tristan da Cunha Islands. Philosophical Transactions of the Royal Society, Series B **249**:273-360.

Wace, N. M., and M. W. Holdgate. 1976. *Man and Nature in the Tristan da Cunha Islands*. International Union for Conservation of Nature and Natural Resources Monograph **6**:1-114.

Wilkins, G. H. 1923. Report on the birds collected during the voyage of the Quest (Shackleton-Rowett Expedition) to the southern Atlantic. Ibis **5**:474-511.

Wikelski, M., J. Foufopoulos, H. Vargas, and H. Snell. 2004. Galápagos birds and diseases: invasive pathogens as threats for island species. Ecology and Society **9**: 5-14.