Influences of environmental change on the eco-evolutionary dynamics of an insular bird *Zosterops lateralis*

A thesis submitted for the degree of Doctor of Philosophy

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Abstract

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The colonisation of islands exposes species to novel biotic and abiotic conditions, that can produce convergent adaptations in morphological and life history traits. One phenotypic pattern, the "island rule", states that initially large bodied species evolve smaller body sizes on islands and smaller species become larger. The underlying mechanisms for this pattern are likely to be complex, and depend on demographic variables and interactions among different phenotypic traits. In this thesis I evaluate mechanisms that may explain evolution of larger body sizes in insular birds by examining the influence of intrinsic and extrinsic factors on morphological and life history traits, and population dynamics of an insular passerine bird, using empirical and modelling approaches. Examining growth, a key determinant of body size, I found that altricial birds tend to grow slower on islands. Intriguingly, a simple integral projection model I analysed showed that the optimal pathway to larger body size was to grow faster. However, the model did not account for more subtle processes, such as within-individual optimisation of resource allocation. This is possibly occurring, as nestling growth variation was not proportional to parental care expenditure. Additionally, larger nestlings and juveniles had higher survival, while survival for all age classes was density-dependent. My findings suggest that island birds may achieve large body sizes by prioritizing offspring quality through slower growth and that size advantages are particularly important at early life stages.

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Author contributions

I declare that this thesis, '*Influences of environmental change on the eco-evolutionary dynamics of an insular bird Zosterops lateralis*' is my own work. The contribution of other authors to any of the manuscripts is clearly stated below. None of the work included has been submitted, in whole or in part, in any previous application for a degree.

CHAPTER ONE

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CHAPTER TWO

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EMS, TC and SMC generated and developed the research idea. EMS implemented data collection, performed data analysis and wrote the manuscript. TC and SMC contributed to the interpretation of results and gave comments at various stages of the manuscript.

CHAPTER THREE

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EMS, TC and SMC generated and developed the research idea. EMS designed and implemented data collection, data analysis and wrote the manuscript. TC and SMC contributed to the interpretation of results and gave comments at various stages of the manuscript.

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EMS, SMC and TC generated and developed the research idea. JK collected the data. EMS performed data analysis and wrote the manuscript. TC and SMC contributed to the interpretation of results and gave comments at various stages of the manuscript.

CHAPTER FIVE

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EMS and TC generated and developed the research idea. EMS performed data analysis, model construction and wrote the manuscript. TC contributed to the interpretation of results and gave comments at various stages of the manuscript.

CHAPTER SIX

Authors: Erik M. Sandvig

Table of Contents

CHAPTER ONE **1**
General Introduction

CHAPTER TWO **17**
The effect of insularity on avian growth rates and implications for insular body size evolution

CHAPTER THREE **39**
Insular nestling growth and its response to parental care

CHAPTER FOUR **67**
The influence of climatic variation and density on the survival of an insular passerine Zosterops lateralis

CHAPTER FIVE **93**
Life history variation and insular body size evolution in birds: an approach using integral projection models

CHAPTER SIX **115**
General discussion

BIBLIOGRAPHY **121**

CHAPTER ONE

General introduction

The colonisation of islands presents species with a novel environment, characterised by a distinct set of biotic and abiotic conditions (MacArthur & Wilson, 1967; Williamson, 1981; Grant, 1998a). These novel conditions have generated an array of convergent adaptations (Grant, 1998b; Blondel, 2000; Clegg et al., 2002; McNab & Ellis, 2006; Losos & Ricklefs, 2009; Covas, 2016). However, the mechanisms underlying some of these insular adaptations are still poorly understood. To understand the ecological and evolutionary drivers of these adaptations requires characterisation of interacting phenotypic traits. In my thesis I will investigate how intrinsic and extrinsic factors influence morphological and life history traits, and population dynamics of an insular passerine bird, using empirical data and modelling approaches to evaluate mechanisms by which small birds are thought to evolve to larger body sizes on islands.

I begin by presenting the 'island rule', an interesting morphological pattern that is thought to be a product of the unique environmental conditions species experienced upon colonizing islands. I then discuss the influence of abiotic and biotic changes on life histories, ecological and evolutionary processes and the interaction of these processes, followed by an introduction into the field of eco-evolutionary dynamics. I will introduce Integral Projection Models (IPMs), a useful tool to study the dynamics of life history and demography, and an interesting framework to apply for studying the dynamics behind insular body

size evolution. Finally, I will describe my study system and my thesis framework.

The Island Rule

Island environments often vary in systematic ways compared to mainland areas, resulting in recurring selection pressures and repeatable phenotypic change in many organisms (Grant, 1998a). These insular conditions are: a consistent and mild climate, availability of ecological niches, low predation and interspecific competition, high population density and high intraspecific competition (MacArthur & Wilson, 1967; Williamson, 1981; Grant, 1998b). Insular populations, across many taxa, exhibit systematic changes in morphology, demography, behaviour, colouration, immune response and life-histories compared to mainland populations (Adler & Levins, 1994; Blondel, 2000; Clegg et al., 2002; Covas, 2012; Novosolov et al., 2013; Doutrelant et al., 2016; Loiseau et al., 2017). These changes are termed the 'insular syndrome'. One of the responses to the novel conditions found in insular environments is the "island rule", which states that large species tend to evolve to smaller body sizes on islands and smaller species tend to get larger (Foster, 1964; Van Valen, 1973; Lomolino, 1985). There is a large body of literature that support this rule in terrestrial vertebrates (Case, 1978a; Lomolino, 2005; Lomolino et al., 2012, 2013) (for exceptions to the "rule" see: Itescu et al., 2014; Meiri et al., 2011, 2008, 2006). Birds also follow the "island rule", with bill and body size increasing in initially small forms, and decreasing in initially larger forms (Clegg and Owens, 2002, Lomolino, 2005). Hypotheses to explain increases in size of initially small-bodied species include size-related advantages when ecological

niches broaden (Scott et al., 2003; Schlotfeldt & Kleindorfer, 2006; Myers et al., 2009), and when agonistic encounters increase in high density populations (Robinson-Wolrath & Owens, 2003; Mathys & Lockwood, 2009; Förschler & Geiter, 2010). These pathways suggest that evolution toward larger phenotypes in size on islands could be linked to differences in the biotic environment between mainland and island settings. In addition to potential changes in behaviour, in order to achieve larger body sizes on islands life history change would also be expected, since body size is inherently related to the rate and length of growth. However, information on growth rates of insular populations remains scarce.

There is ample evidence that insular bird populations appear to have wider ecological niches and foraging behaviours than their mainland counterparts (Diamond, 1970; Alerstam et al., 1974; Cox & Ricklefs, 1977; Scott et al., 2003). Furthermore, there are many studies that report insular morphological shifts in traits related to foraging ecology, such as bill size and shape (Grant, 1965; Abbott, 1974; Clegg et al., 2002). However, populations reported to have wide ecological niches are actually constituted of many individual specialists (Price, 1987; Werner & Sherry, 1987; Scott et al., 2003). The occurrence of different types of individual specialists is not consistent with the idea that selection favours a larger generalist form on islands. Thus, there is currently little empirical evidence to support the idea that broad scale patterns of increased size in initially small birds is due to widening of the niche (Scott et al., 2003; Clegg, 2009).

Densities on islands are typically much higher than on the mainland (MacArthur et al., 1972). The shift in biotic conditions from mainland to island, where interspecific competition reduces and intraspecific competition increases, is thought to favour larger body sizes in birds. Being larger provides a competitive advantage in agonistic encounters, increased access to resources, higher survival probabilities (Clegg et al. 2008) and potentially higher reproductive success (Kikkawa, 1980a; Kikkawa & Wilson, 1983; Pafilis et al., 2009). This hypothesis has received support in insular silvereyes, where larger individuals are more dominant and have higher over-winter survival (Robinson-Wolrath & Owens, 2003), as well as in sparrows and kiskadees (Mathys & Lockwood, 2009; Förschler & Geiter, 2010).

Life history variation

Life history traits describe the key patterns of growth, maturation, reproduction and survival of organisms; and research in life history variation focuses on how selection acts on these interacting traits to maximize fitness over the life cycle (Stearns, 1992; Roff, 2002). Relationships between life history traits and body size are widely recognized and generally measures of body size are positively associated with fitness (Shingleton, 2011). Using a life history approach, Palkovacs (Palkovacs, 2003) theorised that the magnitude of shifts in the individual growth rate curve and the reaction norm describing age and size at maturity, determine the direction and magnitude of body size shifts in insular species. When release from predation pressure is the predominant driver of growth rates and age and size at maturity, body size increases are expected. In contrast, when food limitation is the predominant driver size decreases are

expected. Central to this model, and a unified understanding of the ‘island rule’, is the prediction that life history strategies undergo changes.

Population are immersed in a continuously changing environment, both in its abiotic and biotic components. Variation in these components is what I will be referring to as environmental change. For example, food limitation is a key driver in avian life history variation, influencing offspring growth rates, survival and fecundity (Martin, 1987, 2014a; Sofaer et al., 2018). Biotic factors such as predation are also a widely recognized driver of life history changes through selection on growth rates, survival and influencing fecundity (Martin et al., 2011; Martin, 2015). Increases in predation risk should results in faster growth to increase chances of survival (Cheng & Martin, 2012). Another biotic factor that can play a key role in life history variation is population density.

Density is frequently used as a surrogate of the level of intraspecific competition for resources within a population (Furness & Birkhead, 1984; Festa-Bianchet et al., 1998; Lewis et al., 2001; Amundsen et al., 2007). Density-dependence occurs when life history traits, such as survival, fecundity and growth, change with density (Milner et al., 1999; Coulson, 2001). Examples of this are decreases in survival at high densities due to food limitation (McCallum et al., 2000b), and adaptations in growth rates, time at maturity and reproductive investment when experimentally manipulating densities in guppies (Reznick et al., 2012). As suggested by this last example, life history traits are closely interrelated.

Throughout an individual's life they must partition the resources they acquire between the nutritional costs of growing, survival and reproducing. Life history traits are inherently connected through the constraints involved in this partitioning and trade-offs are made as a result. For example, adults must balance the heavy cost of reproduction with those of reducing mortality through maintenance and predator avoidance (Stearns, 1992). A well-known pattern of covariation among life history traits places species on a slow-fast continuum of life-history variation (Saether & Bakke, 2000). At the slow end of the continuum, species show slower development, lower fecundity and higher survival; typically, long-lived species. At the fast end species mature early, have higher fecundity and lower survival. As discussed above, insular species are generally exhibit the traits of species at the slow end of this continuum (Covas, 2016).

Population dynamics

The life history responses elicited by environmental change can additionally influence a population's demographic rates. Climatic fluctuations, are recognized as a major driver of ecological change, affecting phenology, distribution, and population dynamics of species, and species interactions (Parmesan, 2006; Stenseth et al., 2002; Walther et al., 2002). Understanding the influence of climatic variables on population dynamics is important because of the need to predict the consequences of human-induced global climate change on biological processes (Karl & Trenberth, 2003). Climatic fluctuations influence populations primarily through changes in rainfall and temperature (Stenseth et al., 2002). Variation in rainfall can drive fluctuations in productivity and survival, principally via its influence on food availability (Lima et al., 1999;

Grant et al., 2000; Owen-Smith et al., 2005). Changes in temperature can have direct effects through thermoregulation (Welbergen et al., 2008), or indirect effects through changes in phenology and food availability in terrestrial (Parmesan, 2007) and marine ecosystems (Marinovic et al., 2002; Parmesan, 2007). Rainfall can also directly influence population growth, interacting with and exacerbating the negative effects of temperature on survival (Milner et al., 1999).

Many studies link local weather to changes in bird populations (Sæther et al., 2004). The impact of local weather on population size during breeding season operates on the number of young recruiting into the population, while weather during the non-breeding season impacts adult and juvenile over-winter survival (Sæther et al., 2004). However, identifying local weather measures that succeed in capturing the complex dynamics between climate and ecological processes in some cases can be challenging (Hallett et al., 2004). Instead, many studies use climatic indicators of El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) that influence weather on a large scale (Holmgren et al., 2001; Ottersen et al., 2001; Stenseth et al., 2002). These indicators have been used to study how climate fluctuations influence survival (Milner et al., 1999; Sillett & Holmes, 2002; Barbraud & Weimerskirch, 2003), reproductive success (Nott et al., 2002) and synchrony of population dynamics across large geographical regions (Post & Forchhammer, 2002). Many of these large-scale climatic patterns generate long-term cycles, and are useful variables to study the interaction and consequent effect of density-dependent and climatic changes on population dynamics.

Evolution in island birds has also been linked to abiotic changes. In particular, islands in the Pacific Ocean are greatly influenced by climatic events like El Niño/Southern Oscillation (ENSO). This phenomenon is closely related to food availability for birds and thus to population growth (Grant et al., 2000). Research in Darwin's finches of the Galápagos has documented how changes in environmental conditions, linked to ENSO events, can influence the direction of selective pressures on bill size in response to seed resources in drought vs. non-drought years (Grant & Grant, 1995). The seasonality of climatic conditions on the islands and the recurring extremes in dry and wet conditions brought about by ENSO events are thought to be one of the main drivers of strong selective pressures and consequently the adaptive radiation of finch species in the Galápagos (Grant, 1985). By examining the consequences of abiotic factors on the ecological dynamics and selective pressures in differing environmental conditions we may gain insight into mechanisms of insular evolution.

One of the main biotic drivers of population dynamics is population density variation, that has the potential to influence the ecology and evolution of a species in several ways. Density-dependence can interact with stochastic environmental variation (Forchhammer et al., 2001) to generate population dynamic signatures. In rodents, large population density fluctuations have been attributed to density-dependent processes interacting with rainfall fluctuations (Lima et al., 1999). Studies of ungulates have provided evidence of differential effects of population density across sex and age classes, where high densities exacerbate the effect of weather on survival of susceptible age and sex classes (Coulson et al., 2001).

Abiotic and biotic factors also influence population dynamics through their interactions. Changes in breeding phenology, brought about by warmer spring temperatures, can lead to a mismatch between consumers and their resources, causing decreased survival and breeding success (Visser et al., 1998; Przybylo et al., 2000; Lane et al., 2012; Plard et al., 2014). In contrast, rising temperatures in spring can lead to earlier emergence from hibernation in yellow-bellied marmots, causing higher body mass and consequently increased survival rate, due to longer growing seasons (Ozgul et al., 2010). Climatic fluctuations that interact with biotic processes like food availability, can have either positive or negative effects on population dynamics, influencing survival and fecundity linked to food availability or increasing mortality from harsh weather (Robinson et al., 2007). In some studies, the relationships between climatic conditions and vital rates are correlative (Smithers et al., 2003) and in others, mechanistic processes have been identified, where abiotic and biotic drivers interact (Milner et al., 1999).

Environmental change influences on Evolution

Environmental changes, through its influence on life history and demography, can also drive evolutionary processes. For example, climatic variation is thought to be responsible for the biogeographical trends in body size known as Bergmann's Rule (Bergmann, 1847). Latitudinal temperature gradients have been associated with body size clines found throughout endotherms and many ectotherms, where smaller body sizes are presumed to be better adapted to

warmer climates and larger body size do better in colder climates (Meiri & Dayan, 2003; Meiri & Thomas, 2007).

Population density can also be a driver of evolutionary change. An example is density-dependent selection, where there is a differential effect of density variation on individual fitness due to the individuals phenotype (Clarke, 1972). In sticklebacks, disruptive selection is strongest in high-density environments where intraspecific competition is high (Bolnick, 2004). On the other hand, changes in interspecific interactions can also give rise to evolutionary change. Like in the case of Trinidadian Guppies, where guppy life-history evolves according to predator densities (Reznick, 1982). Interspecific competition can also give rise to evolutionary divergence through character displacement. In Darwin's Finches, one species' beak size has been reported to diverge from a competitor species when food supply was severely depleted (Grant & Grant, 2006).

From the previous paragraphs we can conclude that environmental change, both abiotic and biotic, influences a wide array of ecological and evolutionary processes. When abiotic and biotic changes interact, population responses to these changes become more complex. In the next section I will discuss different mechanisms by which populations respond to environmental change and how ecological and evolutionary processes interact.

Eco-Evolutionary Dynamics

Eco-evolutionary dynamics describes the interactions between ecological and evolutionary processes. Populations can simultaneously respond to environmental change via ecological and evolutionary responses (Réale et al., 2003; Ozgul et al., 2009). Observations of simultaneous demographic and phenotypic changes in traits such as body size (Reznick, 1982), suggest that studying dynamics of trait distributions can provide further insight into the mechanisms underlying the demographic and evolutionary responses to environmental change (Ozgul et al., 2012). For example, in Soay sheep, the phenotypic distribution of the population was influenced by the occurrence of harsh winters, linked to climate change, where fewer harsh winters allowed small slow-growing individuals to survive the winters (Ozgul et al., 2009). Evidence that phenotypic distributions can change in the course of a few generations has given rise to a large body of work in the past three decades exploring how these phenotypic changes may also influence changes in ecological dynamics, cementing the bases for what is now the field of eco-evolutionary dynamics (Pelletier, Garant, & Hendry, 2009).

The study of the influences of environmental changes on eco-evolutionary dynamics explores how biotic and abiotic drivers are associated with the fundamental processes of birth and death (Coulson, T. . Benton, et al., 2006). This has been explored by deconstructing the contribution of ecological and evolutionary processes to changes in population demographics (Coulson, T. G. Benton, et al., 2006). Examples of this are how in ungulates, changes in juvenile mass, a key heritable trait, and environmental variables such as climate

and food availability both contribute towards fluctuations in population growth (Ezard et al., 2009); in salmon introduced to a novel environment, variation in habitat quality and adaptive evolution to the novel environment both influenced changes in vital rates, and hence variation in fitness (Kinnison et al., 2008). Additionally, changes in range distribution of species can also be separated into responses attributed to the interaction of ecological and evolutionary forces (Kubisch et al., 2014). Hence, to fully understand eco-evolutionary change we must explore the contributions of ecological and evolutionary dynamics simultaneously.

Integral Projection Models

Integral Projection Models (IPMs) provide a useful framework to study the dynamics of body size and life history traits. IPMs describe the dynamics of continuous phenotypic characters (Easterling et al., 2000) by tracking the association of a character, for example body size, with vital rates over time (Ellner & Rees, 2006; Rees & Ellner, 2009). These dynamics can be described by four functions that explain their relationship with a character, in this case body size: (1) the probability of survival from time t to time t+1, (2) the development of body size among individuals that survive to time t+1, (3) the number of offspring produced at time t that recruit to the population at time t+1 and (4) the body size of offspring at time t+1 when they recruit to the population (Coulson, 2012). These functions can vary across age, sex or any other grouping variables and be parameterized using data commonly collected in long-term individually based mark-recapture studies (Merow et al., 2014; Rees et al., 2014). Furthermore, IPMs can be analysed by means of sensitivity

analysis to examine how model predictions vary as model parameters are altered (Ozgul et al., 2010; Smallegange & Coulson, 2013). Altering the parameters of each function describing the relationship between the life history traits and body size can be used to explore how each function influences the model predictions gaining insight into mechanisms of eco-evolutionary change (Coulson et al., 2010, 2011).

Furthermore, investigating the influence of both biotic and abiotic factors on body size on islands may elucidate predictable eco-evolutionary responses of birds when encountering these novel insular conditions. These novel conditions will have impacts on the life history traits of the species, influencing survival, growth and fecundity rates. A great system to investigate these questions is the silvereye system.

Study System

The population of silvereyes (*Zosterops lateralis chlorocephalus*) on Heron Island, Australia is an ideal system to investigate the links between population dynamics, evolutionary processes and environmental change. It has been studied since the 1960s and accurate morphological and demographic data has been recorded from the individually marked population for most of the last 50 years. The subspecies on the island is 40% larger overall and up to 6 phenotypic standard deviations bigger in some morphological measures, than its mainland counterpart (Clegg et al., 2008). The silvereye population on Heron Island was established sometime in the last 4000 years (Clegg et al., 2008). Comparisons over different timescales suggest they experienced a period of

rapid evolutionary change towards larger body size shortly after colonization, that slowed on approach to the optimum phenotype, followed by small fluctuations in phenotype as the population tracked smaller-scale environmental variation (Frentiu et al., 2007; Clegg et al., 2008). Silvereyes are an altricial species, meaning that offspring require care and feeding by their parents during the nestling stage (Starck & Ricklefs, 1998). Altricial birds grow in a sigmoidal pattern, increasing in rate until an inflection point, then decreasing and nearing an asymptote shortly after fledging (Ricklefs, 1968). In silvereyes individuals continue growing a small amount during the juvenile stage. Heron Island is subject to climatic fluctuations associated to broad scale climatic patterns such as El Niño events, as well as the impact of tropical cyclones (McCallum et al., 2000b; Clegg et al., 2008) (Australian Bureau of Meteorology). The latter are known to cause large population size reductions followed by rapid recoveries within a year after the event (McCallum et al., 2000b). However, morphological trait changes show no evidence of being influenced by cyclone occurrences and drift most likely does not have an opportunity to affect phenotypic distributions because of rapid recovery after cyclone-induced population decreases (Clegg et al., 2008). The breeding population fluctuates between 225 to 500 individuals (McCallum et al., 2000b). Compared to mainland *Zosterops* densities (Davies, 2010), the densities on the island are high (Kikkawa, 1976). Silvereyes populations are sexually monogamous (Robertson et al., 2001) and form social hierarchies (Kikkawa et al., 1986), where young dominant individuals have higher over-winter survival rates than young subordinate individuals (Kikkawa, 1980b). The island is a low predation environment for silvereyes, but with some predation by silver gulls (*Chroicocephalus*

novaehollandiae), eastern reef herons (*Egretta* sacra) or buff-banded rails *(Gallirallus philippensis*) on nestlings or fledglings (Catterall et al., 1982, EMS and SMC Pers. Com.)

Framework of the thesis

The main objective of this thesis is to improve our understanding of how the interactions between environmental, demographic and life history processes influence body size in insular passerines, and how the responses to these interactions may contribute to a better understanding of how small birds become larger in insular environments.

The following data chapters 2 – 5 are presented in the style of journal articles.

CHAPTER TWO

In this chapter I address a gap in our knowledge of the general life history patterns in insular environments. I conduct a meta-analysis of nestling growth rates in altricial birds, to assess divergence in patterns and drivers of growth rates between island and mainland populations. I discuss our finding in light of its implications for insular body size evolution.

CHAPTER THREE

In this chapter I describe the nestling growth patterns of the population, their association with measures of parent body size and parental care expenditures, and compare patterns of growth between an island and mainland population at

the intraspecific level. Understanding these links is important because body size is regulated by mechanisms that control the length and rate of growth.

CHAPTER FOUR

In this chapter I use a 15-year capture-mark-recapture dataset to investigate the influence of environmental variation, namely density and climatic variation, on the survival of individuals and how they differ between age classes across the life cycle.

CHAPTER FIVE

In this chapter I use a modelling framework to address questions of the role of life history shifts in the body size and population dynamics in an insular environment. I construct and analyse a phenotypic IPM using long-term data, for three age classes, incorporating the relationship of key life history traits with body size. This way, we can use these models to predict changes in body size when altering life history traits.

CHAPTER SIX

This chapter completes the thesis with a synthesis of our findings and discusses suggestions for future directions of research to address some of the outstanding questions that remain in insular body size evolution.

CHAPTER TWO

The effect of insularity on avian growth rates and implications for insular body size evolution

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Abstract

Island populations often differ in consistent ways from their mainland counterparts with respect to their ecology, behaviour, morphology, demography and life-history characteristics; a set of changes referred to as the 'island syndrome'. To understand the ecological and evolutionary drivers of the island syndrome requires characterization of suites of interacting traits. While patterns in some types of traits, e.g. body size, are well characterised across a range of taxa, key gaps remain. Growth rate is one such trait, being an important determinant of both increases and decreases in body size, and can vary with changes in predation pressure and food limitation; two factors that are known to differ between mainland and island environments. Using a phylogenetic meta-analytic approach, we characterise differences in growth rates among mainland and island altricial bird populations, controlling for environmental factors. We found a trend toward slower growth on islands in small-bodied (<1kg) bird species. This is consistent with the idea that the pattern of body size increases in small-bodied island colonists is associated with the evolution of slower growth combined with shifts in age and size at maturity in relaxed predation regimes.

Introduction

Islands are excellent systems to study the factors that influence life history variation, as island populations are exposed to a suite of environmental conditions that differ in predictable ways to their mainland counterparts (Grant, 1998b). These include lower predation pressure (Losos & Ricklefs, 2009), and a shift in the balance of inter- versus intra-specific competition (Blondel, 2000). Indeed, these features of insular environments are often invoked to explain a series of repeated adaptations across a wide range of taxa, referred to as the 'island syndrome' (MacArthur & Wilson, 1967; Grant, 1998b; Losos & Ricklefs, 2009). In birds, changes in morphology (a tendency towards medium body size) (Clegg et al., 2002) and decreased plumage dimorphism (Doutrelant et al., 2016), behaviour (increased tameness, increased intraspecific aggression) (Grant, 1998b; Clegg et al., 2002; Robinson-Wolrath & Owens, 2003), demography (increased population densities) (MacArthur et al., 1972; Wright, 1980; Blondel et al., 1988) and life history characteristics (a shift to a slower life history strategy) (MacArthur & Wilson, 1967; Grant, 1998b; Blondel, 2000; Covas, 2012, 2016) are features of the island syndrome. Slower life history strategies are manifested in lower fecundity, increased adult survival [5], longer developmental period (the amount of time the offspring stay in the nest) and higher investment in offspring seen in island species compared to their mainland counterparts (Bosque & Bosque, 1995; Covas, 2012). However, growth rate variation (i.e. the rate at which nestlings gain mass during development) has been a neglected component, despite being a key life history descriptor in itself (Starck & Ricklefs, 1998), with feedback links to other life history variables e.g. survival (Dmitriew, 2011; Maness & Anderson, 2013).

Importantly, investigating insular growth rates may shed light on other features of the island syndrome, such as evolutionary shifts in body size (Palkovacs, 2003).

Studies of continental bird species show that growth rates vary widely among species (Ricklefs, 1968, 1973). This variation has been attributed to a suite of biotic factors, such as nest predation risk, food limitation, clutch size, adult body size, nest type, phylogenetic relationships, and biotic and abiotic factors associated with latitude (Lack, 1968; Case, 1978b; Starck & Ricklefs, 1998; Remeš & Martin, 2002; Dmitriew, 2011; Martin et al., 2011; Cheng & Martin, 2012). Of these factors, nest predation risk is often considered the predominant environmental driver of variation in growth rates across geographic regions, where selection favours faster growth rates in environments with high nest predation rates, thereby minimizing offspring mortality (Martin et al., 2011; Cheng & Martin, 2012). When food is limited and parental feeding rates drop, offspring growth rates may also decrease (Martin, 1987). This effect can be compounded by high predation risk, as adults may make fewer provisioning trips to their offspring to reduce the chances of a predator discovering a nest (Martin et al., 2011). However, even under such conditions, nestlings can increase growth rates, presumably through changes in resource allocation (Martin et al., 2011). The effects of other factors include slower growth rate with smaller clutch sizes when adult survival is high (Ghalambor & Martin, 2001; Martin et al., 2011); slower growth in larger bodied species (Ricklefs, 1968); faster growth in species that have enclosed nests which decreases energy allocation needs for thermoregulation (Martin et al., 2017); and faster growth

rates in higher latitude populations with longer daylight hours (Ricklefs, 1976; Remeš & Martin, 2002). Slower growth is generally accompanied by longer nestling periods when comparing species of similar size, because growing at a slower rate requires more time to reach a particular size (Ricklefs, 1968).

The 'island rule', describes the trend for initially large-bodied species to evolve smaller body sizes on islands and initially small-bodied species to evolve larger body sizes (Lomolino, 2005), a biogeographic rule that has been of long-running interest (Clegg et al., 2002; Lomolino, 2005; Meiri et al., 2006, 2011; Price & Phillimore, 2007; Boyer & Jetz, 2010). Using a life history approach, Palkovacs (Palkovacs, 2003) theorised that the magnitude of shifts in the individual growth rate curve and the reaction norm describing age and size at maturity, determine the direction and magnitude of body size shifts in island dwelling species. When release from extrinsic mortality (e.g. lower predation pressure) is the predominant driver of growth rate and age and size at maturity, body size increases are expected, as could be argued to be the case for initially small-bodied species (Fig 1a). In contrast, when food limitation is the predominant driver, as may apply to initially large-bodied species, size decreases are expected (Fig 1b). Central to this model, and a unified understanding of the 'island rule', is the prediction that growth rates on islands decrease. Slower insular growth rates in island versus mainland populations would be expected under the typical insular conditions of reduced (or absent) predation pressure in food limited environments (where intraspecific competition is high and area is limited on smaller islands; the generality of food limitation on larger islands is less clear), and where smaller clutch sizes are produced

(where adult survival is high and parental investment is spread across a longer developmental period). However, this prediction hinges on the assumption that the developmental stage that nestlings achieve before fledging remains unchanged. If nestlings fledge at a later developmental stage, then growth rates themselves may be similar for island and mainland representatives (O'Connor, 1984).

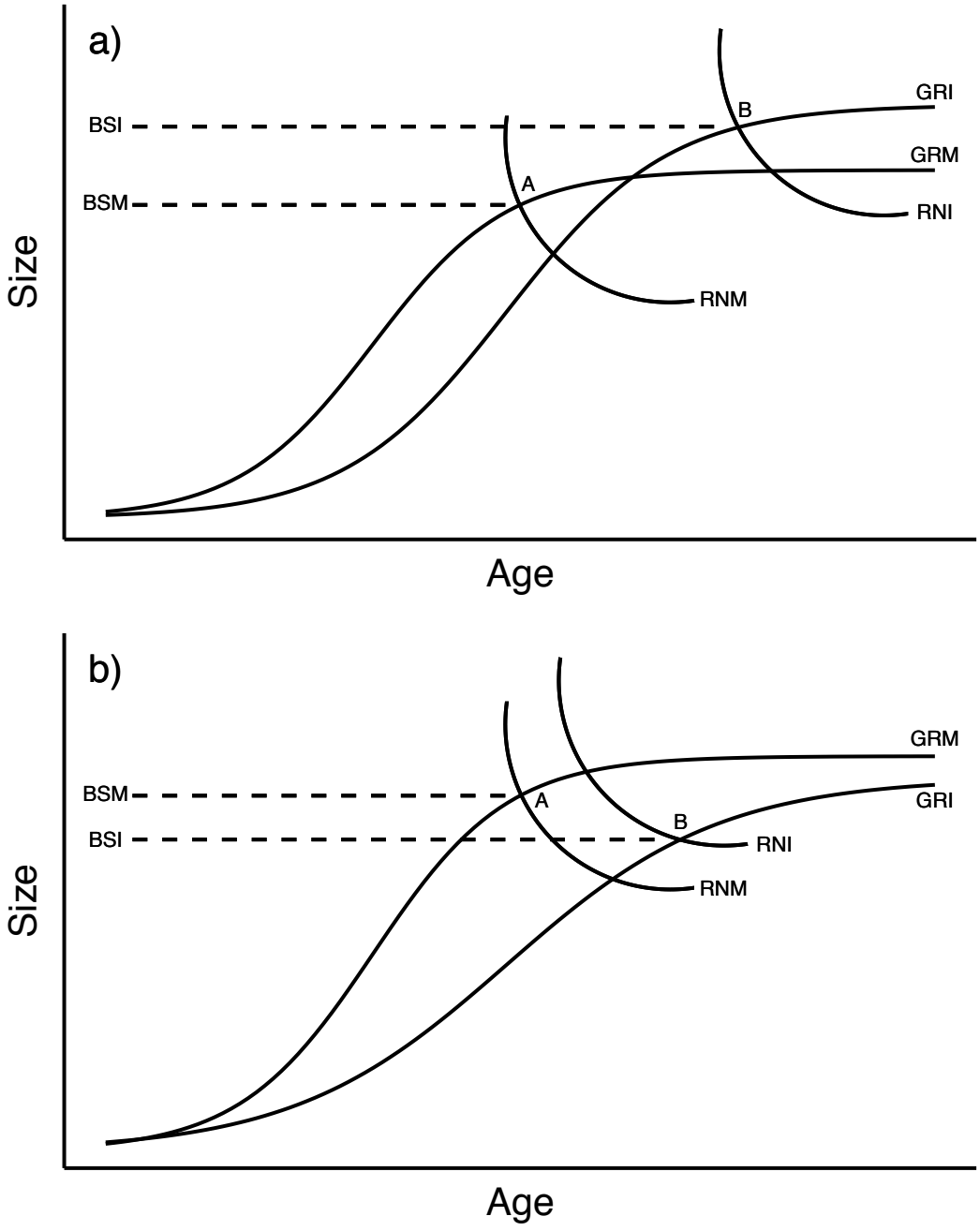


Figure 1. Theoretical prediction of avian body size changes from mainland to island environments as a product of shifts in growth rates and the reaction norm determining age and size at maturity. This follows Palkovacs (2003) general description of changes in adult body size on islands (BSI) compared to the mainland (BSM), but modified for avian growth rates specifically. a) When predation release is the dominant ecological driver, the effect of reduced extrinsic mortality (shift from RNM to RNI) is larger than the effect of lower growth rate (shift from GRM to GRI) resulting in increases in insular body size. b) When food limitation is the dominant ecological driver, the effect of reduced growth rates is larger than the effect of reduced extrinsic mortality, resulting in smaller insular body sizes. Note body size at maturity is determined by the intersection of the growth rate curve and the reaction norm of age and size at maturity (A and B).

Here we examine growth rate variation across a wide range of bird species to investigate the effects of insularity on growth rates. We use a phylogenetic meta-analytic approach using data from published literature to determine the difference between growth rates of altricial birds from mainland areas and islands, controlling for the effects of latitude, clutch size, adult body size and nest type among species. We then compared variation in growth rates among islands including additional covariates of island area and isolation. Island area and isolation determine the equilibrium number of species present; small isolated islands are expected to be more depauperate than large islands close to mainlands (MacArthur & Wilson, 1967). Hence these variables act as broad proxies for the potential for interspecific competition and predation. We ask the

following questions: (a) are growth rates of insular altricial bird populations slower than mainland ones? (b) are the variables that explain among-island variation in growth rates similar in relative importance as those that explain mainland-island variation? We then discuss these findings with reference to insular body size evolution.

Methods

Data Collection

We conducted a literature search and compiled a database of nestling mass growth rates of terrestrial altricial birds covering studies published from 1910 to 2016. We first searched for publications from the Web of Science using combinations of the following keywords: “bird*”, “nestling*”, “offspring”, “growth rate*”, “develop*”, “rate*”, “growth”, “postnatal” and “island”. From the resulting list of publications, we scanned the abstracts and selected all studies that mentioned descriptions of nestling growth or the species’ breeding biology. These studies were then read in more detail and growth rate estimates extracted. The bibliographies of these studies were then cross-checked for references to other studies that may contain estimates of nestling growth. Finally, we systematically searched through species accounts in three comprehensive bird handbooks that provided detailed information on growth rates (The Birds of North America, Handbook of Australian, New Zealand and Antarctic Birds and The Birds of Africa)(Rodewald, 2015; Higgins et al., 1990-2006; Brown et al., 1982-2013).

We restricted the analyses to studies that reported growth rate values (*k*) estimated from a logistic model, as transformations of these values are comparable among species (Ricklefs, 1968). *k* is the maximum relative growth rate at the point of inflection of a logistic curve and is obtained from variations of the Richards logistic equations (i.e. logistic, Gompertz and Von Bertalanffy) (Tjørve & Tjørve, 2010). Each of these equations fixes the inflection point at a specific rate (50%, 37% and 30%, respectively), therefore to allow direct comparisons, we transformed all *k* constants for equivalence with the most widely used logistic equation using the method of Ricklefs (1973). We excluded studies that only reported growth in terms of grams per day, as interspecific variation in these rates is not directly comparable. Mean growth rate was averaged when reported for each sex separately. Bird Orders for which there was data of only mainland, or only island, populations were excluded from the analysis to avoid biasing the representation of growth rates among groups of species. Parasitic species were excluded from the analyses because the growth rates of their offspring vary widely depending on their host species (Remes, 2010). Body size affects growth rate and the direction of insular body size evolution depends on the ancestral starting point; size reduction typically occurs if ancestral body sizes are > 1 kg, and size increases if < 1 kg (Lomolino, 2005). Hence any trends in insular growth rate changes may be obscured if this directionality is not considered. As only 12 cases of growth rate estimation were available for birds >1kg, we restricted the analysis to birds with average adult body size < 1 kg.

Associated variables recorded for each growth rate were the sample size and the location, latitude of the study population, whether it was on an island or mainland, and for island populations, the distance to the nearest continent and the area of the island was log transformed (taken from the Island Directory http://islands.unep.ch/) or using Google Earth if not stated in the study (Anon., 2017)). We excluded islands larger than 250.000 km^2, because of their similarity to mainland environments. For each species, mean adult body mass (grams) and modal clutch size was taken from the *Handbook of the Birds of the World Alive* (http://www.hbw.com/)(del Hoyo et al., 2017), and log transformed to conform to assumptions of normality. If mass was given for each sex, a mean was calculated. If modal clutch size was not given, average clutch size was used. Geographic co-ordinates were not reported in 13 cases, so were approximated from the known distribution of the species and general country or region descriptions provided in each study. We found multiple growth rates for 47 species, all of them mainland populations. When more than one growth rate was found for the same latitude we averaged the *k* values and counted it as one data point un the analysis. The full dataset and code is accessible at https://figshare.com/s/02ce3dbf88e1e3118925. Publication bias was unlikely to affect the distribution of effect sizes of our meta-analysis since reporting growth rates is unlikely to depend on its magnitude and is not subject to statistical significance (Koricheva et al., 2013).

Statistical Analyses

We applied a Bayesian mixed effects phylogenetic meta-analytic approach (Hadfield & Nakagawa, 2010), implemented in the package MCMCglmm

(Hadfield, 2010) in R version 3.4.0 (R Core Team, 2017) to analyse variation in growth rates (*k*). To test our hypothesis of an effect of insularity on growth rates, we fitted linear generalized mixed models, were we assume *k* to be normally distributed. First, we fitted a general model including fixed effects of insularity (i.e. mainland or island population), latitude, clutch size, body size and nest type (open or enclosed) using the entire dataset. Next, we restricted the dataset to include growth rates of island species only to investigate environmental influences on insular growth rates among island populations. We fit a model including fixed effects of latitude, island area, distance to mainland, clutch size, body size and nest type. Both models included the random terms: study, species (to account for variation introduced by having multiple measurements for 55 species), phylogeny (to account for similarity due to shared evolutionary history), and measurement error (to account for variation introduced by sample size and to weight the effect sizes accordingly). The measurement errors were approximated using the inverse of the study sample size (i.e. 1/N), following the recommendation of Hadfield et al. (2010), as values of variance, or statistics from which it can be estimated, were reported in a very low proportion (9%) of studies. Using the taxonomy of Jetz et al. (Jetz et al., 2012),we randomly sampled 100 phylogenetic trees from BirdTree.org (www.birdtree.org) for the 213 species included in the study using the “Ericson All Trees” as the source (a consensus tree can be found in the supplementary information). To account for phylogenetic uncertainty we fit the two statistical models tested over the 100 trees and extracted the mean density of the combined posterior distribution using the package mulTree (Guillerme & Healy, 2014). We used an uninformative prior with variance, *V*, set to 1 and belief parameter, *nu*, to 0.002,

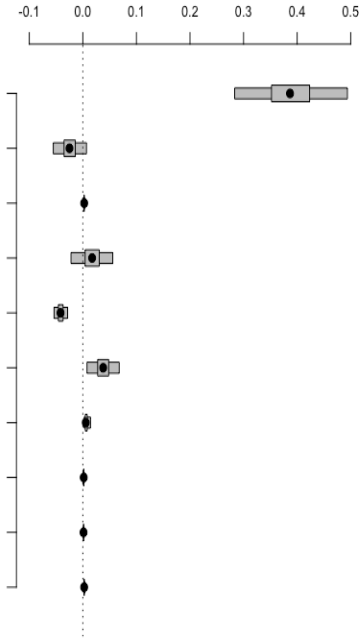
for both fixed and random effects (Hadfield, 2010). We ran two chains for 500,000 iterations, with a thinning value of 300 and a burn-in of 10,000. All models were required to have an effective sample size greater than 1000 and we checked for convergence between model chains using the Gelman-Rubin statistic, the potential scale reduction, where all models were required to be below 1.1 (Gelman & Rubin, 1992). We considered fixed effects to be statistically significant when the 95% credible interval did not span zero. We estimated measures of goodness-of-fit by calculating marginal and conditional R-squared for each model (variance explained by the fixed effects only and that of combined fixed and random effects, respectively) according to (Nakagawa & Schielzeth, 2013).

Results

General Model

The general model assessing the effect of insularity on growth rates included 264 growth rates (231 mainland and 33 island populations) from 213 species across 198 different studies (marginal R-squared = 0.32, conditional = 0.85). There was a strong phylogenetic signal in the data (total variance explained = 35%) (Fig2). After accounting for phylogeny, significant effects were seen for latitude (faster growth at higher latitudes), nest type (faster in species with open cup nests) and adult body size (slower in larger species)(Table 1). Growth rates in island species tended to be slower though the effect was marginally nonsignificant. Clutch size had a nonsignificant effect. For size and direction of effects see Table 1. An additional model including only the mainland data was tested, which gave the same results as general model.

Table 1. Potential predictors of growth rate variation in 213 species (n=264) of altricial birds: population type (island or mainland), latitude, clutch size, adult body size, nest type (open or enclosed). Estimates (black circles) are modal values from 100 models, and the error bars (grey shading) show the lower and upper 95% and 50% confidence intervals from the 100 models.

	estimate	lower CI	upper CI	posterior distribution
intercept	0.387	0.283	0.494	
island	-0.025	-0.055	0.007	
latitude	0.002	0.002	0.003	
log(clutch size)	0.017	-0.022	0.056	
log(body size)	-0.042	-0.054	-0.029	
nest type: open cup	0.038	0.008	0.068	
phylogenetic.var	0.005	0.002	0.014	
species.var	0.002	0.0001	0.003	
study.var	0.001	0.0001	0.002	
residual.var	0.002	0.002	0.004	

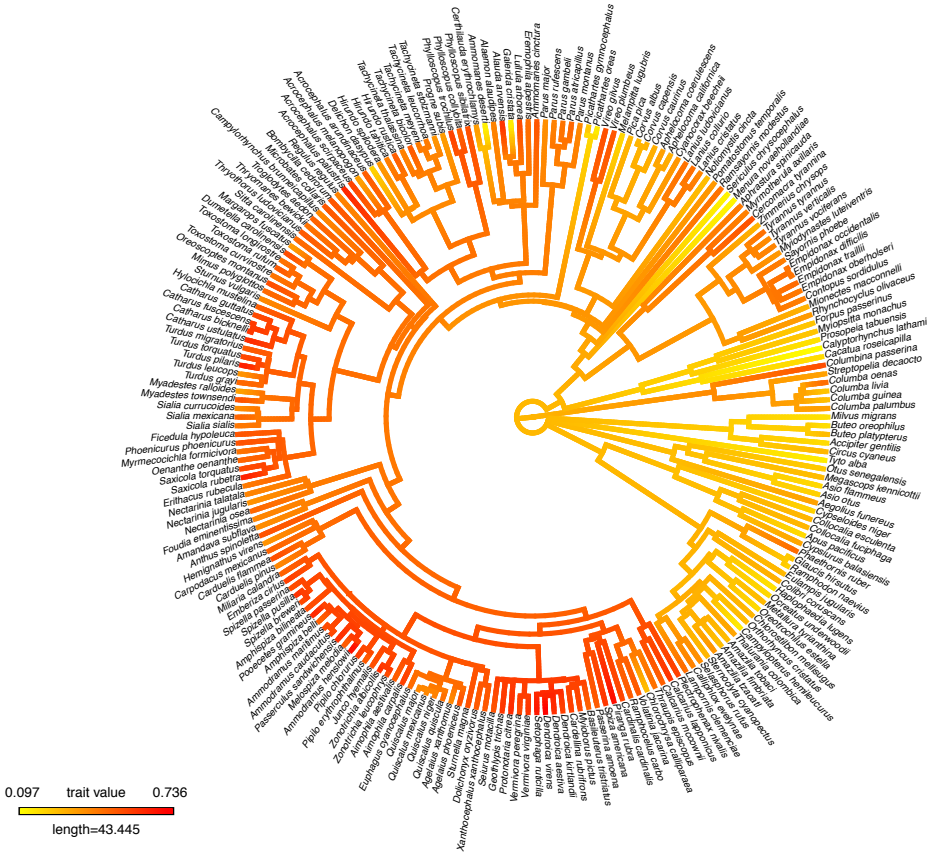


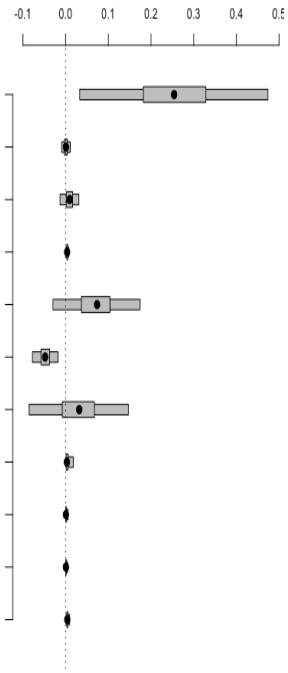
Figure 2. Growth rates (*k*) of 213 altricial bird species depicted on a phylogenetic tree, chosen at random from the 100 trees (for methods of tree construction see (Jetz et al., 2012)). Growth rates range from 0.097 to 0.736 and show a strong phylogenetic signal (51% explained variance). Dark red depict fast growth rates and light yellow depicts slower growth rates.

Island Model

The model included 33 growth rates from 30 species in 27 studies (marginal R-squared = 0.52, conditional R-squared = 0.77). A moderate phylogenetic signal was noted (total variance explained = 17%), and latitude had a significant positive effect (faster at higher latitudes) and adult body size a significant negative effect (slower in larger species) on insular growth rates. All other variables were not significant (Table 2).

Table 2. Potential predictor of growth rate variation on islands in 30 species (n=33) of altricial birds: island area, distance of the island to the mainland, latitude, clutch size, body size, nest type (open or enclosed). Estimates (black circles) are modal values from 100 models, and the error bars (grey shading) show the lower and upper 95% and 50% confidence intervals from the 100 models.

	estimate	lower CI	upper CI	posterior distribution
intercept	0.254	0.033	0.474	
log(island area)	0.001	-0.009	0.011	
log(distance to mainland)	0.009	-0.013	0.032	
latitude	0.004	0.001	0.007	
log(clutch size)	0.074	-0.030	0.174	
log(body size)	-0.048	-0.078	-0.018	
nest type: open	-0.032	-0.086	0.0147	
phylogenetic.var	0.003	0.0002	0.018	
species.var	0.001	0.0002	0.006	
study.var	0.001	0.0002	0.005	
residual.var	0.004	0.002	0.010	



Discussion

Our comparative, phylogenetically controlled analysis of growth rates in altricial bird species found a trend towards slower growth rates in species that are predicted to increase their body size in insular environments. In line with Palkovacs' (Palkovacs, 2003) hypothesis, this empirical data supports the idea that initially small birds achieve larger insular body sizes by growing at a slower rate over a longer growth period, facilitated by a low predator environment.

Growing at a slower rate and over a longer period allows for larger and higher quality offspring to be produced by decreasing oxidative stress damage during development (Monaghan et al., 2009), decreasing the per nestling energy requirements on parents (Ricklefs, 1984) and increasing the total amount of provisioning time (Ricklefs, 1968). This may translate to better survival and reproductive outcomes in high-density insular populations where intraspecific competition is likely to be elevated. Finally, assuming that the 35 island bird population growth rate estimates used in our study are a representative sample of insular altricial birds, then even a small increase in sample size would likely result in significance of the insular trend to be noted.

Our finding of faster growth rates at higher latitudes, regardless of whether the data set included all comparisons, or only comparisons among island populations, is in line with previous studies (McCarty, 2001; Kilpatrick, 2002; Rose & Lyon, 2013). Increased resource availability at higher latitudes (Ashmole's hypothesis (Ashmole, 1963)), and increased daylight hours during the breeding season at higher latitudes (such that parents make greater total feeding trips to the nest) have been proposed as explanations of this pattern. More recently Rose & Lyon (Rose & Lyon, 2013) found that variation in daylight hours explained intraspecific latitudinal variation in growth rates and clutch size, while resource availability did not.

An inverse relationship between growth rates and adult body size has also been documented by other authors (Remeš & Martin, 2002), however, as growth is indexed independently of body mass when calculating *k* (Ricklefs, 1968), the

cause of this relationship is difficult to determine. Remes & Martin (Remeš & Martin, 2002), suggested this negative relationship may be due to larger birds having higher survival rates (Saether, 1989; Martin, 1995) and, with increased adult survival under reduced extrinsic mortality, a lower energy expenditure on reproduction is expected (Martin, 2014b). Faster growth rate in open-cup nesters may be explained by higher nest predation risk selecting for faster growth to decrease nestling mortality in open- vs. enclosed-nest types. However, recent findings argue that thermal benefits of enclosed nests are an important selective pressure favouring faster growth rates, and outweigh benefits of reduced nest predation risk (Martin et al., 2017). We did not find a significant effect of clutch size, but this may be due to the positive correlation between clutch size and latitude, such that including both variables obscured the possible effect of clutch size on growth rate.

Comparison of growth rates among island populations showed that the effects of latitude and adult body size maintain their influence on growth rate variation in insular environments. The lack of influence of other abiotic variables, distance to mainland or island area, on growth rates may reflect that these variables were not adequate proxies of variation in predator and competitor numbers as anticipated. A lack of support for the influence of nest type on insular growth rates may reflect the expected decrease in selective pressure from reduced nest predation risk. However, the lack of support for these variables should be taken with caution as it may be due to the modest number island growth rates rather than there being no effect.

It is important to mention that the high variability in the quality of reporting growth rates and associated data meant that close to half of the studies we found were excluded from this meta-analysis. Most studies published after Ricklefs' influential paper (Ricklefs, 1967) report estimates of *k*, and thanks to the work done by Ricklefs (Ricklefs, 1976), Oniki (Oniki & Ricklefs, 1981) and Starck & Ricklefs (Starck & Ricklefs, 1998) calculating *k* from previously published raw growth data, many more species were able to be included in this study. However, a large number of studies that expressed growth in grams per day without enough detailed data to be reanalysed to estimate *k* still remain. Furthermore, an important aspect that led to excluding many studies that did report *k* was not reporting any type of variance statistic or sample size, when at least one is needed for weighting effect sizes in meta-analyses. To improve the comparability of growth rates in future studies, we encourage researchers to report all growth curve parameters together with a measure of their variance. Finally, Tøjrve and Tjørve (Tjørve & Tjørve, 2017) have developed a "Unified" family of models to describe growth patterns, improving upon the traditional logistic, Gompertz and von Bertalanffy models, that the authors argue produce the most realistic estimate of growth parameters. The adoption of this new family of models would greatly improve the quality and comparability of growth rate statistics.

Our study highlights the biogeographic and taxonomic gaps that limit our ability to form a more nuanced understanding of variation in altricial avian growth rates, particularly where it relates to the island rule. Growth rate estimates were predominantly from the Order Passeriformes, with only a moderate

representation from five other Orders. Island population growth rate estimates were surprisingly under-represented in the literature. Hence, whether the tendency for slower growth in insular birds noted in the sample used in our study can be generalised to a wider range of bird Orders, and for bird species that evolve towards smaller insular sizes, remains to be established. Because of the significant negative relationship between adult body sizes and growth rate seen here and in other studies (Ricklefs, 1968; Remeš & Martin, 2002), one might predict that species that undergo size reductions on islands may have faster growth rates compared to their mainland counterparts. However, such a response may be countered by food limitation imposed by space restriction and lower species diversity on islands. Furthermore, as more growth data becomes available, our understanding of the effects of insularity on growth rates would benefit from additional analyses comprising intraspecific comparisons between mainland and island populations. Finally, more empirical information is needed to understand how reduced predation versus potentially reduced resource availability on islands shapes variation of avian growth rates across species and hence how this will translate into body size changes across a broad range of species.

Data accessibility

The datasets used in the full and island mixed models, including references to the original studies, phylogenetic trees and the code to run the analysis can be downloaded from https://figshare.com/s/02ce3dbf88e1e3118925.

Acknowledgements

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Supplementary Information

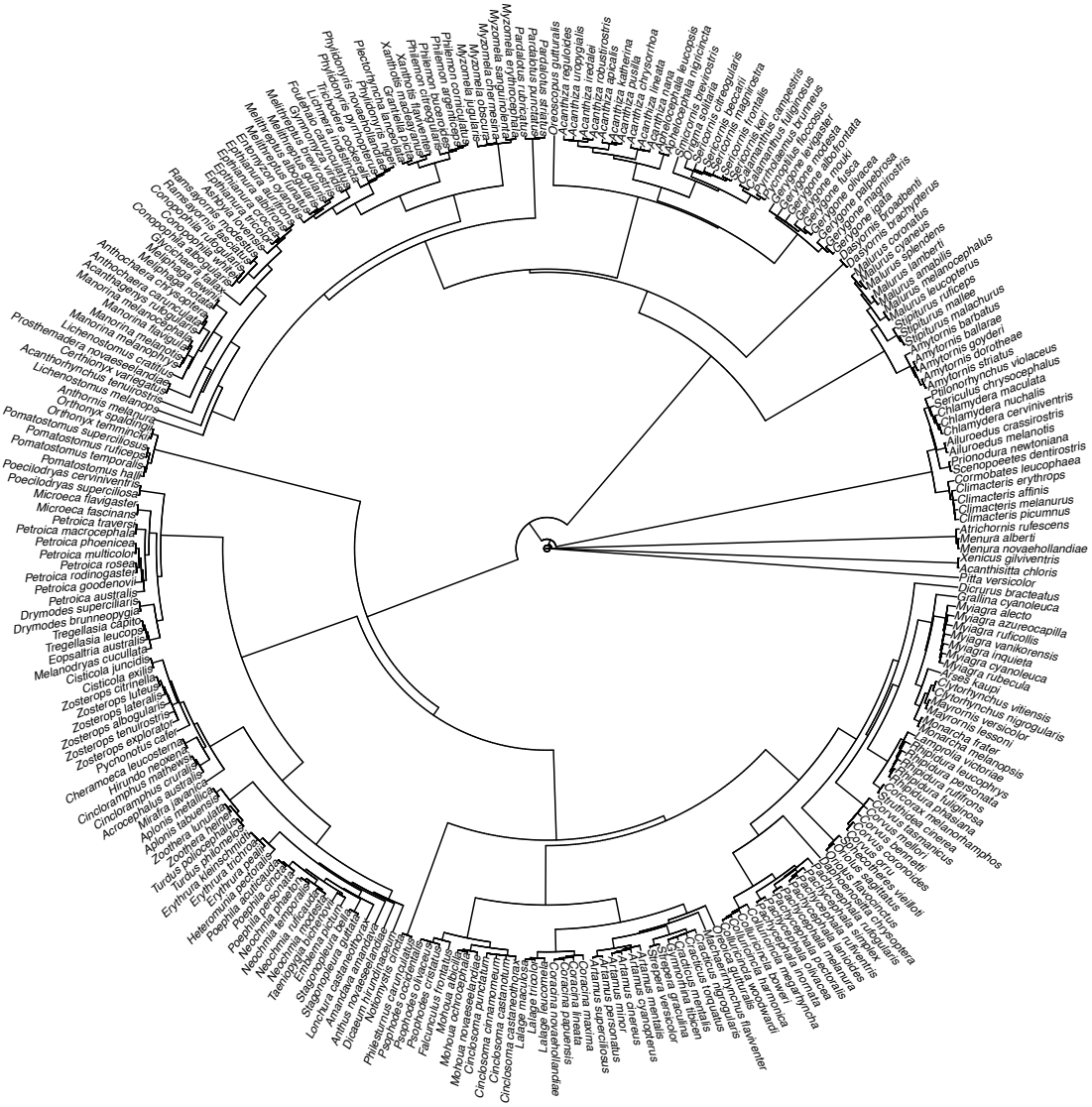


Figure S1: Consensus tree constructed from the 100 trees used in the analysis. This is done by identifying the phylogeny with the minimum sum of squares distances to the 100 trees.

CHAPTER THREE

Insular nestling growth and its response to parental care

Erik M. Sandvig, Tim Coulson & Sonya M. Clegg

Abstract

The rate at which offspring grow while in the nest can have consequences for survival and reproductive output as an adult, and is known to vary widely among and within species. This variation is thought to be an adaptive response to cope with environmental variation. The principle environmental factors affecting growth are food availability and predation risk, predominantly acting as constraints on level of parental care. Islands pose an interesting system to explore growth rate dynamics, because the characteristic insular features of high population densities and depauperate predator diversity translate into a potentially food limited environment with low predation risk. Insular environments typically produce populations with slower life history strategies and body size increases in small-bodied species, features that are likely to be mediated by growth rate. Hence, exploring growth rate variation can contribute to a mechanistic understanding of key insular adaptations. We describe the growth patterns of an insular population of silvereyes and how they relate to parental size and parental care expenditure, by measuring per-nestling provisioning rates and time spent brooding, and compared growth patterns between island and mainland populations. Neither parental size nor parental care expenditure explained nestling growth rate, even though food acquisition is thought to underpin much of growth rate variation. We found no statistical difference in growth between mainland and island, although the island rate tended to be slower. Even though this is in line with predicted insular adaptations, the mechanisms by which slower growth produces larger body sizes on islands remains unclear. Future research should explore how food acquisition translates into physiological allocation of resources in insular

populations, and incorporate a detailed look into the quantity and quality of food items on a spatial and temporal scale.

Introduction

Growth rates are an important life history trait that can have long-term consequences for individual fitness (Gebhardt-Henrich & Richner, 1998) and can vary widely both among and within species (Ricklefs, 1968; Starck & Ricklefs, 1998). Understanding the drivers influencing this variation informs our knowledge of adaptive evolution of life history traits (Dmitriew, 2011) and how they could be linked to morphological changes. In birds, most studies of growth rates and drivers of variation have focused on mainland populations (Sandvig et al. in prep). However, in insular systems key drivers of growth rate variation, namely predation pressure and food availability, differ from the mainland in repeatable and predictable ways (Grant, 1998b) (shifts in food availability may be less clear for larger islands). Thus, islands are a valuable system for studying patterns of growth and the factors that influence them in an environment that is consistently different from the mainland.

Although life-history theory predicts that species should grow at their physiological maximum due to survival and reproductive advantages of larger body sizes, slower growth rates are commonly observed (Dmitriew, 2011). This is attributed to constraints on maximum physiological rates of growth by environmental conditions (Dmitriew, 2011). Factors influencing variation in parental care, namely the energy expenditure involved in provision of food and thermoregulation to chicks, can significantly affect offspring growth rates (Starck & Ricklefs, 1998; Martin et al., 2011; Sofaer et al., 2018). Lower provisioning rates, and hence slower growth rates may occur. Slower growth may also produce a longer nestling period for nestlings to be able to reach full

development (Starck & Ricklefs, 1998). The amount of resources an offspring is able to acquire is not only constrained by food availability but also by adult mortality risk incurred by predation pressure. However, although slower growth rates from lower provisioning rates (i.e. number of feeding visit to the nest by parents) in high predation environments may be expected, nestlings are capable of growing faster by prioritising resource allocation to traits that allow them to increase their chances of survival by escaping predation (e.g. feather growth) (Martin et al., 2011). Additionally, growth rates may be slower in smaller clutches, when adult survival is high, because adults would be expected to prioritize their own survival over parental care (Ghalambor & Martin, 2001). This can be compounded by food limitation, which results in smaller clutch sizes. Growth rates can also vary depending on the timing of breeding and brood number, where early breeding generally favours faster growth by matching peak food availability (Sedinger & Flint, 1991). Where parental care is not limited by food availability the relationship between growth rates and brood size is predicted to have a slope approximating zero (Tremblay et al., 2003; Martin et al., 2011). The relative importance of these environmental factors, and their interactions, determine the direction and magnitude of the selective pressures acting upon growth rates in a given population.

There are a suite of convergent adaptations termed the ‘insular syndrome’ which have been attributed to the repeated environmental conditions found on islands. Among the characteristic attributes of insular environments are reduced (or absent) predation pressure and food limitation (due to high population densities in a small area). In birds, changes in morphology, behaviour,

colouration, immune response, and a shift towards slower life history strategies are attributes of the 'insular syndrome' (Clegg and Owens, 2002; Blondel, 2000; Doutrelant et al., 2016; Loiseau et al., 2017; Covas, 2012). Insular adaptations in reproductive traits also include shifts in growth rates, where insular populations tend to grow slower than on the mainland (Sandvig et al., in prep) a feature which may underpin body size evolution on islands (Palkovacs, 2003). However, detailed descriptions of insular growth patterns, their relationship with environmental drivers, and intraspecific comparisons between island populations and their mainland relatives are still lacking (Sandvig et al. in prep).

Here we characterise the post-natal growth rate of an insular population of silvereyes (*Zosterops lateralis chlorocephalus*) on Heron Island, Australia. This population maintains high population densities (McCallum et al., 2000b), exceeding those found on the mainland (Lenz, 1990; S. J J F Davies, 2010), which could induce food-limiting constraints on growth rates. There is low predation risk on the island; occasionally nestlings are predated by buff-banded rails (*Galliralus philippensis*), silver gulls (*Chroicocephalus novahollandiae*) or eastern reef egrets (*Egretta sacra*)(Catterall et al., 1982b, EMS and SMC Pers. Obs.). The subspecies has diverged morphologically (up to 40% larger body size) from its mainland ancestor since colonizing the islands it currently inhabits less than 4000 years ago (Clegg et al., 2008), hence is an interesting population to study in light of general associations between growth rate and body size. Here we estimate the parameters that describe the growth curves of a suite of biometric traits, the relationship between mass growth rates and parental body size, brood size, brood number and hatch date to growth rates,

and compare insular growth rates to a limited dataset available from mainland silvereyes. We characterise parental care investment using proxies of food delivery rates and brooding behaviour over the nestling period and determine its relationship to growth rates. We predict nestling growth rates to be (1) faster in nestlings with larger parents, assuming an allometric scaling of parents' capacity of acquiring food with body size; (2) slower with increasing brood size, as per nestling provisioning would decrease in a food limited environment; (3) slower in subsequent broods and later hatch dates, as food availability should decrease later in the breeding season; (4) slower in the insular population due to lower predation pressure and food limitation. Finally, (5) we predict provisioning to increase over the nestling period and brooding time to decrease, in accordance with increasing energy allocation requirements and development of endothermy of nestlings, respectively.

Methods

Study Area

Heron Island (23^{o} 26' S, 151^{o} 57' E) is a wooded island of the Capricorn-Bunker Group, covering an area of approximately 16 ha, located 70km off the eastern Australian Coast on the southern tip of the Great Barrier Reef. The weather is subtropical with a mean annual rainfall of 1034.3 mm (1956-2007), and mean max and min temperatures are 26.2 $^{\circ}$C and 20.8 *C (1962-2007), respectively (Australian Bureau of Meteorology, www.bom.gov.au). On the island, the Capricorn silvereye (*Zosterops lateralis chlorocephalus*) is the only regularly breeding passerine (Kikkawa, 1976) and individuals have been colour-banded since 1964 (Kikkawa, 1997). The breeding season of silvereyes starts in late

September (exceptionally early September) and ends in early March (exceptionally early April) (Sandvig et al., 2017). A cup shaped nest is built by both parents in the crook of a branch between 0.5 m and 13 m high, predominantly in *Pisonia grandis*, the dominant tree species, but will nest in most other tree, bush and herbaceous species found on the island. Incubation starts the day after the last egg is laid. Parents take turns incubating for a period of 10 to 14 days. Both parents share provisioning of nestlings, feeding them an assortment of insects and pieces of fig; the latter in an increasing proportion as they grow (Catterall et al., 1982). The nestling period lasts 10 to 15 days. Clutch size ranges from one to four eggs (exceptionally six), with a mode of 3 eggs.

Nest searching and nestling measurements

Nest searching was conducted during October and November of 2015 and October to December of 2016. Nests were checked every three days during building and egg laying stages, and daily from a day before expected hatch date to determine an accurate hatching date. Nestlings were measured every two days between 14:00 and 17:30, beginning on day two (hatching day = day zero) until day eight. Nests were not approached after day 8 to prevent premature fledging. Measurements for wing length, tarsus length, posterior culmen length (from tip to posterior end of nasal orifice), anterior culmen length, width, and depth (from tip to anterior end of nasal orifice) were taken with callipers and weight was recorded using a 20-gram (±0.06 grams accuracy) spring scale.

Growth rates

All statistical analyses were performed in R version 3.4.0 (R Core Team, 2017), with the packages 'minpack.lm' (Elzhov et al., 2016), 'lme4' (Bates et al., 2015), 'BSDA' (Arnholt & Evans, 2017) and base statistical functions. We fitted a range of statistical models to each biometric measurement. The logistic model is the most widely used equation for growth rates in passerines, and has proven to be a useful tool for interspecific comparisons of growth rates (Starck & Ricklefs, 1998). However, recently a four-parameter version of the Richards model (Tjørve and Tjørve 2010; Tjørve and Tjørve 2017), termed the "Unified Richards" (U-Richards) model, has been proposed as an improvement over the three-parameter logistic model. While the logistic equation fixes the inflection point at 50% of the asymptote, the U-Richards model includes an additional parameter that determines the trait value (i.e. the proportion of the asymptote) at which the inflection point is fit, allowing for more flexibility in the description of the shape of the growth curve (Vrána et al., 2018). We estimated growth curve parameters by fitting the biometric measurements from the nestlings to both a logistic model of the form Equation 1, and a U-Richards model of the form Equation 2, where *A* is the upper asymptote, *d* is the proportion of the upper asymptote at inflection, k_l *and* k_u are the maximum relative growth rate (at inflection), t is age in days, and T_i is the age at the point when the curve inflects (Tjørve and Tjørve 2010).

Equation 1:

$$A/(1+\exp(-k_l(t-T_i)))$$

Equation 2:

$$(1 + (d-1) * \exp\left(-\frac{k_u(t - T_i)}{d^{\frac{d}{1-d}}}\right))^{1/(1-d)}$$

The estimated relative maximum growth rate parameters k_l and k_u (from the logistic and U-Richards models, respectively) have the advantage of being comparable by a simple transformation: $k_u = k_l/4$. We used AIC to compare performance of models (Akaike, 1974), considering differences in AIC (i.e. ΔAIC) greater than 2 to be evidence of one model performing better than another (Burnham & Anderson, 2002). We considered P values < 0.05 to show statistical significant.

To test for a relationship between parental body size and nestling growth rates we performed a principal component analysis (PCA) on adult biometrics to capture, with the first Principal Component (PC1) capturing body size (see results). We used the base function *princomp* and included measurements of mass, wing, tarsus, posterior and anterior culmen length and anterior culmen width from a five-year dataset (2012-2016, n=859). PC1 was averaged for each pair because parental care is shared. We then estimated growth rates (k_l) for individual nestlings using logistic regressions, excluding individuals with less than four measurements and those that decreased in mass in subsequent measurements (n = 44), as the logistic equation cannot properly estimate the parameters under these conditions. We used a generalised linear mixed model (GLMM) to test for the effect of the mean parental PC1 on individual nestling growth rates, including a random effect for nest. A second GLMM was used to

test the effect of brood size on individual growth rates, including a random effect of nest.

To explore variation in nestling mass increases we fit a GLMM with a response variable of mass at time t_i+1 and included fixed effects of mass at time t_i, age, hatching date (a numeric vector starting on the first recorded hatched nestling) , brood size, brood number, year and average parental size (using PC1, detailed above), and random effects of nest and individual identity to account for lack of independence between siblings and repeated measures, respectively.

Nest provisioning

Nests were recorded with action cameras (GoPro 3 Silver, www.gopro.com, San Mateo, California, USA) for two to three hours between 14:30 and 18:30, on each day that nestlings were measured. Cameras were covered in a camouflage tape and positioned between 0.5 and 1 metre from nests and nesting pair behaviour was monitored to ensure camera placement was not detrimental to nest success (no cases of nest abandonment were recorded). The videos were scored for the number of trips made to the nest by both parents and the amount of time spent at the nest on each visit. Provisioning rates were calculated as the number of nest visits per nestling per hour. Time was recorded starting from the first visit of a parent after installing or changing the battery of the camera. The individual parental identity could not be determined as colour bands could not be easily seen in the shaded conditions of the nests; therefore, variables represent combined parental visits. GLMMs with visits per nestling per hour as a function of day, and brooding time as a

function of day, both with a random effect of nest, were fit to test for temporal changes over the nestling period. GLMMs were also fit for individual growth rates as a function of visits per nestling per hour on day four post-hatching and as a function of brooding time on day four post-hatching, both with random effect of nest, to test for an influence of parental effort in provisioning rates and time spent at nest on growth rate variation. We used data from the fourth day post-hatching because this coincided with the age of maximum relative growth (see results). Individual growth rates (k) were log-transformed to fit assumptions of normality; a normal error distribution was used in both models describing growth rate variation.

Island versus mainland growth

To test the influence of insularity on silvereye growth rates, we compared the growth curve parameter estimates for mass of the Heron Island population to that of a mainland population using the only available published data from a population in Western Australia (Booker, 2001). We fit a logistic model (see above) instead of the more descriptive U-Richards model with the additional parameter because of the small sample size from the mainland (n=1-8 birds). We then used a Welch-modified two-sided t-test to test for differences in the estimated growth curve parameters between the insular and mainland mass data.

Results

Nestling growth rate variation

PC1 was interpreted as adult body size with comparable loadings for mass, wing, tarsus, posterior and anterior culmen length, and excluded anterior culmen width, and explained 34.6% of the variance (see supplemental materials). We found no relationship between growth rates of individual nestlings and the average body size PC1 scores of their parents (Figure 1, slope = -0.002 (0.02 SE), t value = -0.14, p = 0.89, n = 67). We found a significant relationship between weight at time t+1 and time t, as well as significant negative effect of hatching date on weight. No effects were found for brood size, brood number, year or average parent size on weight (Table 1). We found no effect of brood size on individual growth rates (Figure 2, slope = 0.07 (0.05 SE), t value= 1.54, p = 0.13, n = 96).

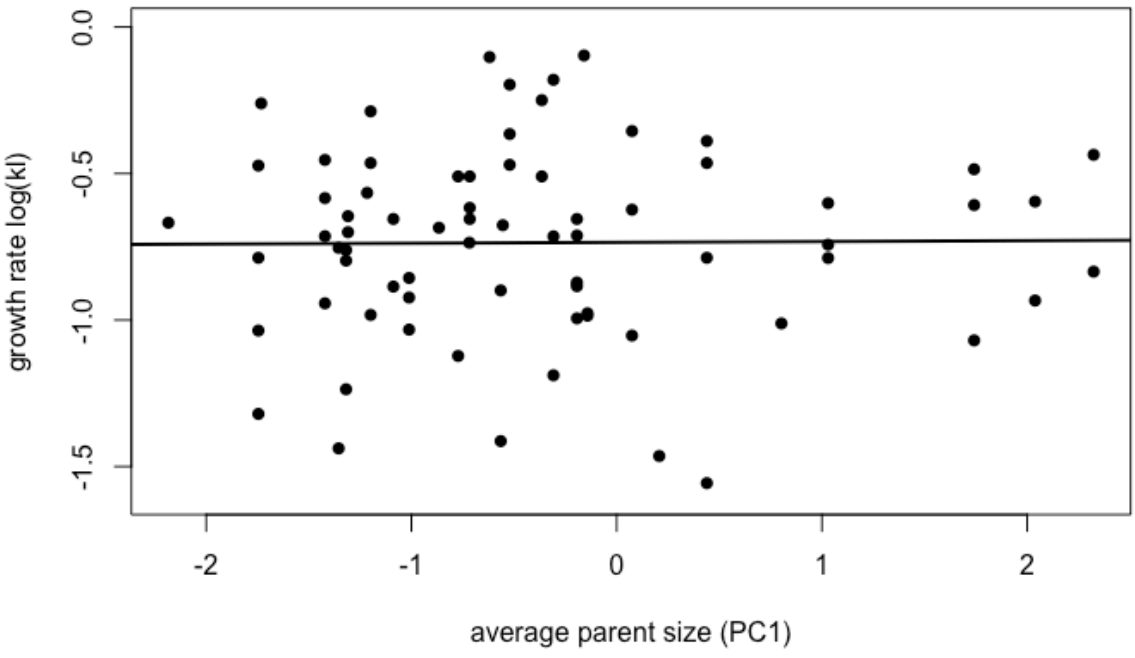


Figure 1. Average parental PC1 scores of each nestling plotted against logged individual nestling growth rates (k_I).

Table 1. Parameter estimates for a GLMM testing the influence of mass (time *t*) on subsequent mass increases (time *t*+1), including fixed effects of day (age), hatch date (a numeric vector starting on the first recorded hatched nestling), brood size, brood number, year and average parental size (using PC1 detailed above). df = 198.

parameters	**estimate (SE)**	**t value**	***p***
intercept	3.94 (0.36)	10.88	<0.001
mass *t* (gr)	0.82 (0.05)	15.5	<0.001
day4	0.61 (0.19)	3.21	0.002
day6	-0.21 (0.3)	-0.70	0.48
hatch date	-0.01 (0.01)	-2.19	0.03
brood size	-0.14 (0.09)	-1.51	0.13
brood number	0.09 (0.14)	0.66	0.51
year (2016)	0.02 (0.13)	0.15	0.88
average parent size	0.02 (0.05)	0.35	0.73

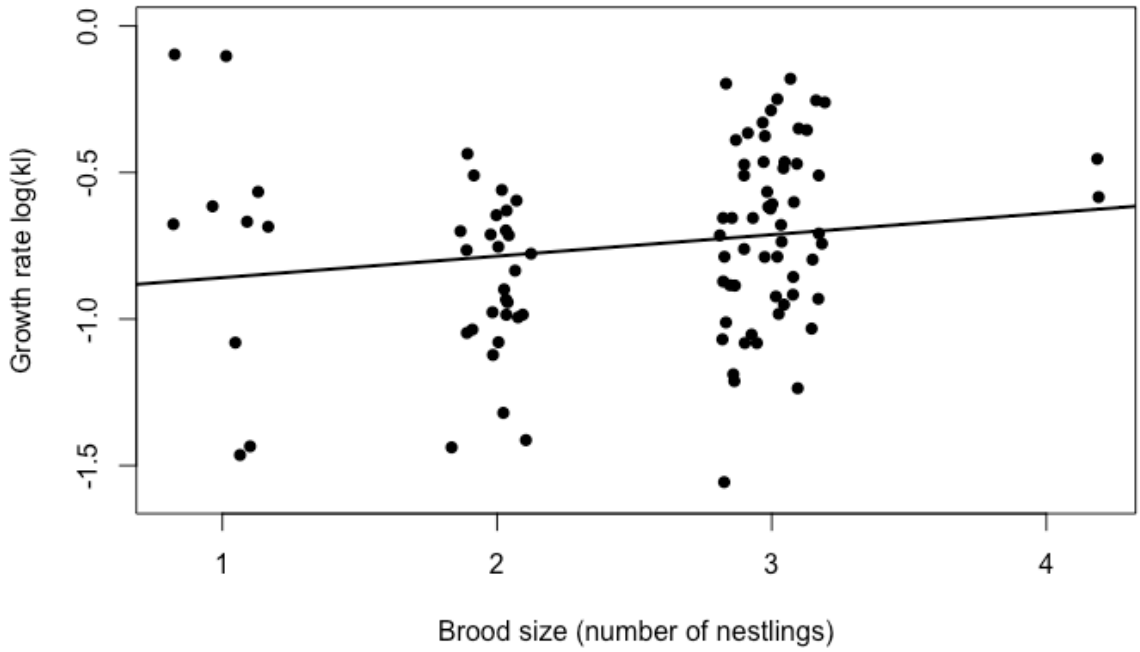


Figure 2. Relationship between individual nestling growth rates (k_l) and brood size. Line is from GLMM of the logged estimate of maximum relative growth rate (k_l) of nestlings as a function of its brood size, with a random effect of nest. Points are jittered along the x axis to improve clarity.

Nest provisioning and nestling growth

We found a significant increase of visits per nestling per hour as the nestling period progressed (Figure 3 (A), slope = 1.08 (0.15 SE), t value = 7.08, p = <0.001, n=77) and a significant decrease in brooding time over the nestling period (Figure 3 (B), slope = -8.19 (1.660 SE), t value = -4.94, p = <0.001, n = 74). We found no relationship between the number of visits per nestling per hour on day four post-hatching and individual nestling growth rates k_l (Figure 4 (A), slope = -0.0001 (0.02 SE), t value = -0.01, p = 0.1, n = 26), and no relationship between brooding time and individual nestling growth rates k_l (Figure 4 (B), slope = -0.0004 (0.002 SE), t value = -0.22, p = 0.83, n = 27).

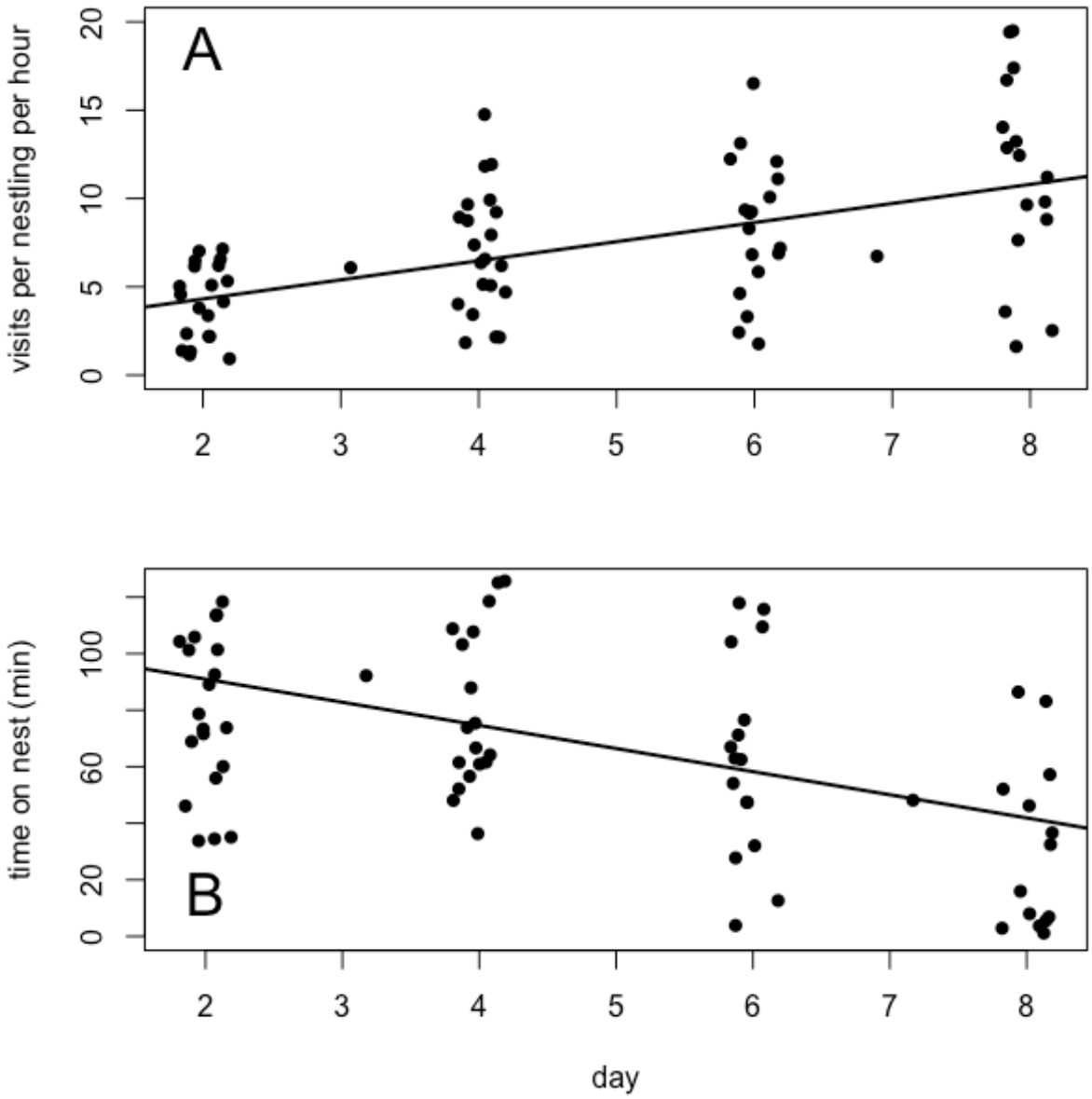


Figure 3. A: Number of visits per nestling per hour by parents to the nest over an 8-day development period. **B**: Cumulative length of time (minutes) that parents are on the nest over the 8-day period. Lines are the model fit from GLMMs of visits per nestling per hour and brooding time, respectively, as a function of day, both with nest as a random factor. Points are jittered along the x axis to improve clarity.

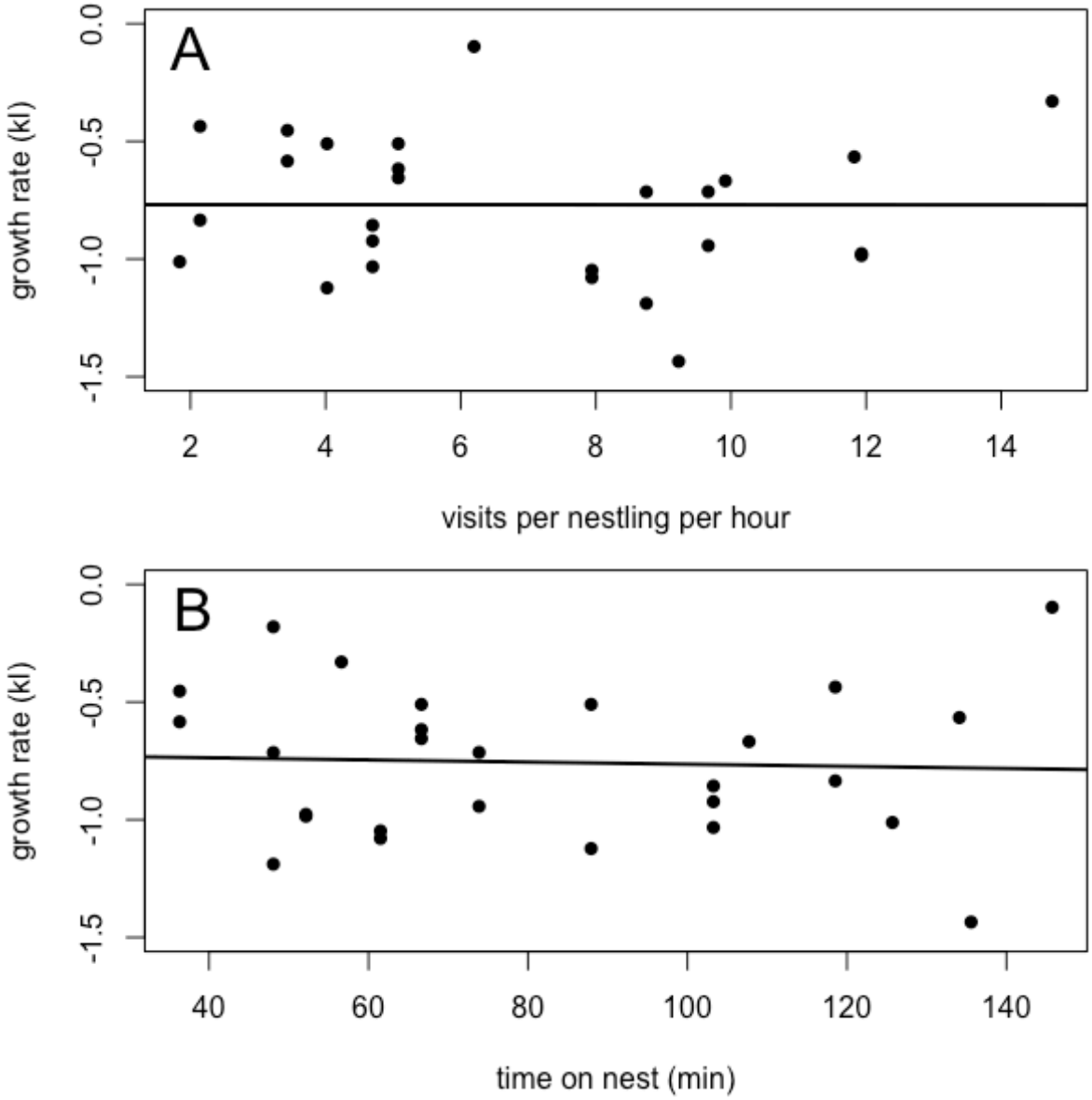


Figure 4. Non-significant relationship between individual maximum relative growth rates (k_l) and (A) the number of visits per nestling per hour to the nest by parents on day four post-hatching and (B) the cumulative length of time parents spent on the nest (brooding time) on day four post-hatching.

Island versus mainland growth

We found a significant difference between estimated asymptotic mass of the insular and mainland mass data, but not for wing length. There were no significant differences between estimated growth rates (k_l) or time at inflection in mass or wing data (see Figure 5, Table 2 and Table 3 for parameter estimates and t-test results). There were no differences in performance between U-Richards and logistic model methods for any of the biometrics traits. However, the standard errors in the U-Richards model estimates of anterior culmen width and depth are considerably large (Supplementary information).

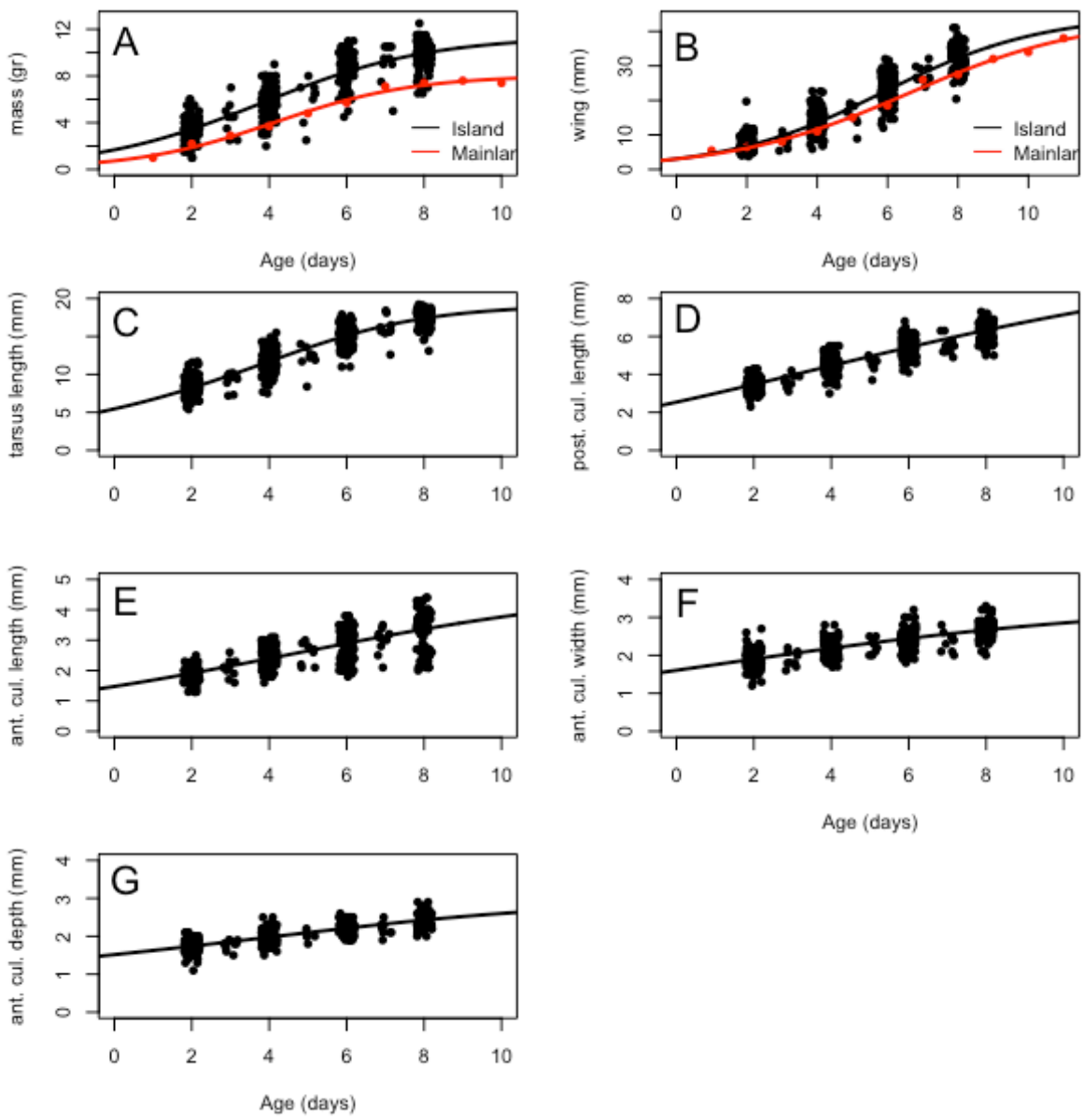


Figure 5. Growth curves of the best performing model for nestling biometric measurements. Using the U-Richards model: A, mass, B, tarsus, D, posterior culmen length, E, anterior culmen length, G, anterior culmen depth. Using the logistic model: C, wing, F, anterior culmen width. Lines are the predicted values for the best fit growth curve of each trait. Red points and lines shown in A and B show logistic growth curve for a mainland silvereye population. Points are jittered along the x axis to improve clarity.

Table 2. Differences in fitted parameters values of the logistic model for island (n=496) and mainland (n=1-8) mass data assessed using a Welch-modified two-sample t-Test for each parameter: *A* is the upper asymptote, k_l the relative maximum growth rates as inflection, and *t* the time at inflection (days). Standard error is given in brackets.

Parameters	Island mass mean (SE)	Mainland mass mean (SE)	t value	*p*
A	11.39 (0.4)	8.04 (0.23)	7.3	>0.001
k_l	0.46 (0.03)	0.56 (0.05)	-1.61	0.124
t	3.82 (0.19)	4.14 (0.18)	-1.24	0.224

Table 3. Differences in fitted parameters values of the logistic model for island (n=496) and mainland (n=1-8) wing data assessed using a Welch-modified two-sample t-Test for each parameter. *A* is the upper asymptote, k_l the relative maximum growth rates as inflection, and *t* the time at inflection (days). Standard error is given in brackets.

Parameters	Island wing mean (SE)	Mainland wing mean (SE)	t value	*p*
A	44.81 (2.41)	44.14 (2.8)	0.18	0.856
k_l	0.44 (0.02)	0.4 (0.04)	1.16	0.258
t	5.89 (0.28)	6.6 (0.41)	-1.44	0.164

Discussion

Body size adaptations on islands are expected to require adaptations in growth patterns in response to the unique insular environment. Contrary to expectations, the measured maximum relative growth rates of nestlings were not related to their parents' body size, and showed no evidence of being limited by food availability during the breeding season. Growth rates were neither explained by nestling resource acquisition or brooding time, despite them increasing and decreasing with nestling age as expected. Population comparisons revealed that the island growth pattern is not dissimilar to mainland populations, even though there is evidence of the 'island rule' in body size.

Nestling growth rate variation

Although larger adults in this population are more dominant, winning more agonistic interactions in competition for food (Robinson-Wolrath & Owens, 2003), we found no evidence of a relationship between parental body size and their offspring's growth rates. This may be because there is not a clear relationship between per-nestling provisioning rates and nestling growth rates. Thus, even though larger parents may theoretically provision more, this does not directly translate into faster growth in the nests of larger parents. Further efforts should explore how parental care expenditure, in terms of brooding time, and quality and quantity of food delivered to young, varies with the size or dominance status of parents.

The negative effect of hatch date on nestling mass predicts smaller nestlings as the breeding season progresses. This could be expected if the quality of food items decreases throughout the season. Previously, arthropod abundance has been found to decline as the breeding season progressed (Eguchi, 1993). Intraspecific reaction norms of growth rates relative to brood size are predicted to change based on levels of food limitation (Martin et al., 2011). In food-limited environments growth rates are predicted to decrease with increases in brood size, as limited resources are spread thin among larger broods. Our findings suggest that during the breeding season, the island is not a food-limited environment for nestlings. Similar results were found in Chapter 2 for interspecific variation in growth rates, where the lack of an effect of clutch size suggests that food limitation is not a general driver of insular growth rate variation (for the subset of island populations analysed in that study). However, this is not to say that there may not be variability in the quality of food resources on Heron Island during the breeding season (Catterall et al., 1982), as well as spatial and temporal variation throughout the year (Catterall, 1985). Clegg et al. (2008) found reduced overwinter survival, that is likely linked to limited food availability or access (Clegg et al., 2008). In addition, cyclones can have significant detrimental effects on the population on a semi-decadal frequency, with drastic decreases in survival, but rapid recovery in the following year (McCallum et al., 2000a). The effects these extreme climatic events have on the temporal dynamics of food resources on the island are still poorly understood.

Nest provisioning and growth

As nestlings got older they were both provisioned more frequently and brooded for less time as expected. However, neither provisioning rates, nor time spent brooding, where able to explain growth rate variation among nests. This was unexpected because food acquisition is thought to regulate most within-population growth rate variation (Ricklefs, 1976; Konarzewski et al., 1996; Searcy et al., 2004; Killpack & Karasov, 2012). Findings similar to ours have been reported were provisioning rate did not explain nestling mass gain (Sofaer et al., 2018) or mass at fledging (Schwagmeyer & Mock, 2008). Schwagmeyer and Mock (2008) found that the number of food items did not explain the mass at fledgling, but the number of large food items did. On Heron Island, Catterall (1982) found that the proportion of figs to insects fed to nestlings increased as they grew, and pairs that fledged more offspring were older, fed nestlings more insects and nested in areas with higher fruiting fig tree density. This temporal and spatial heterogeneity in the nutritional contents of provisioning adds an additional layer of complexity to the provisioning-growth relationship. An additional explanation could be a mismatch between the acquisition and allocation of food provided by the parents. Nestlings are able to prioritise the allocation of food differentially to different traits during development (e.g. prioritise development of internal organs over flight feathers) depending on selective pressures (Martin et al., 2011). In the case of insular environments, a lower predation pressure may shift allocation prioritisation from fast growth in flight feathers to development of internal organs, possibly resulting in a higher quality fledgling – which would be a desirable attribute in highly competitive insular environments. The lack of support for an effect of brooding time nestling

growth may also reflect a mismatch between the age of maximum relative growth rate and that of the thermal requirements of silvereye nestlings. However, it may also be the case that the limited length of the recordings was not able to explain variation in growth rates, as patterns of parental investment can vary throughout the day (Low et al., 2008). This requires more detailed investigation of parental care with longer periods of recording and information on the thermal requirements of nestlings.

Island versus mainland growth

Given high adult survival (Sandvig et al., 2017), low predation environment (Clegg et al. in prep) and strong intraspecific competition (Robinson-Wolrath & Owens, 2003) in the Heron Island population of silvereyes, maximising phenotypic quality of nestlings by means of slower nestling growth would be expected. However, we did not find a significant difference in growth rates for mass or wing length between insular and mainland populations. A previous comparison between island and mainland populations in a small passerine in North America reported slower growth in the island population (Sofaer et al., 2013, 2018). However, the mainland population was located at higher latitude, which, considering the shifts in abiotic factors at higher latitudes (i.e. higher productivity, longer photoperiod and shorter breeding season), may explain the reported faster growth rate on mainland. It is important to note that the sample size for the available mainland silvereye data was small and thus, our results may be due to reduced statistical power rather than a non-significant difference between growth rates. Additional growth data for a mainland population on the east coast of Australia will be collected during the 2018 breeding season and

included in a subsequent analysis in order to obtain more robust results for publication.

Although the U-Richards model performed well in traits of faster growth rates, parameter estimates for traits with slow growth (i.e. bill biometrics) were unrealistic and had large variances. This highlights a possible limitation to the use of this model; however, it is difficult to discern to what extent having a limited number of measurements per nestling might have influenced this. Given these results, we recommend that both three and four parameter models should be fitted and compared to improve confidence in precision of growth estimates.

Conclusions

While most studies have looked into the environmental drivers of nestling growth rate variation by assessing the constraints brought upon by food limitation and predation risk, this study portrays a different perspective, from an island with virtually no predation risk and no evidence of food limitation during the breeding season.

Our results shed light on the complex relationships driving growth rate variation of nestlings in this type of environment. They also highlight the need for a more detailed examination of parental care, looking into the quality and quantity of food items, incorporating the spatial and temporal variation related to dominance hierarchies, and how these resources are allocated physiologically. Finally, extending this study to compare the drivers of growth variation with a mainland population of silvereyes at a similar latitude, with the same level of

detail as suggested above, would provide a firmer understanding of how the selective pressures in local environments shape nestling growth strategies between populations on different evolutionary trajectories.

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CHAPTER FOUR

The influence of climatic variation and density on the survival of an insular passerine *Zosterops lateralis*

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Abstract

Understanding the influence of environmental factors on population dynamics is fundamental to many areas in biology. Survival is a key factor of population biology, as it is thought to be the predominant driver of growth in long-lived passerines, which can be influenced by both biotic and abiotic environmental conditions. We used mark-recapture methods and generalized linear mixed models to test the influence of density and climatic variation, measured at a regional and local scale (Southern Oscillation Index [SOI] and rainfall, respectively), on seasonal variation in survival rates of an insular population of silvereyes (*Zosterops lateralis chlorocephalus*), during a 15-year study period, off the east coast of Australia. We found overall high survival rates for adults and juveniles (81% and 59%, respectively). Local scale climate (i.e. rainfall) and density were the principal environmental factors influencing their survival, both with a negative relationship. A significant interactive effect of density and rainfall influenced survival as they both increased. However, survival remained low when density was at it highest, independent of the amount of rainfall. Nestling survival was negatively influenced by rainfall and density, positively by SOI, and chicks that hatched later in the breeding season had higher survival rates. The regional scale climate variable (i.e. SOI) did not explain survival rates as strongly as rainfall in any age class. Our results contribute to the understanding of insular avian population dynamics and the differential effects of environmental factors across age classes. Climatic predictions expect El Niño events to increase, meaning dryer conditions in eastern Australia, potentially increasing silvereye survival across age classes. However, the long-term effect

of lower rainfall on food availability is unknown; consequently, the outcome of lower rainfall on silvereye survival rates is uncertain.

Introduction

Understanding how climatic variation and density-dependent effects influence population dynamics is a topic of great interest in ecology, particularly as environmental change is occurring at an unprecedented rate (Karl & Trenberth, 2003). Climatic fluctuations can impact populations directly through physiological processes (Forchhammer et al., 1998), as well as through interaction with intrinsic density-dependent processes (Coulson et al., 2001). In birds they have been linked to changes in distribution, phenology, behaviour, morphology and population dynamics (Stenseth et al., 2002; Mazerolle et al., 2005; Chambers et al., 2011; Gibbs et al., 2011). In avian population dynamics, of the main components that govern variation in population growth (survival, fecundity, immigration and emigration), adult survival rate is thought to be the predominant driver of change in growth in long-lived species (Saether & Bakke, 2000). Research has shown that large-scale climate patterns, like El Niño/Southern Oscillation (ENSO), play an important role in bird population dynamics (Jenouvrier, 2013), driving sharp increases and steep declines in population sizes (Gibbs & Grant, 1987; Grant & Grant, 1987a; Sillett, 2000), as well as impacting phenology and breeding success (Grant et al., 2000; Smithers et al., 2003). Thus, to improve our understanding of how climatic variation influences avian population dynamics it is key to understand the links between climate, density-dependence and survival.

ENSO influences climate on a global scale (Holmgren et al., 2001), driving temperature and rainfall patterns measured at a local scale (McBride & Nicholls, 1983). Survival in birds is closely linked to changes in temperature and rainfall

during El Niño events (Nott et al., 2002; Sillett & Holmes, 2002). Furthermore, rainfall may be the most important short-term factor influencing the demography of tropical and subtropical birds, due to increased food availability, linked directly or indirectly to rainfall (Pearce-Higgins et al., 2014). However, in events of extreme precipitation it may decrease breeding success and increase mortality (McDonald et al., 2004). These stochastic environmental fluctuations have been found to interact with density-dependent effects and influence bird demographics, decreasing survival when climatic conditions are harsh and density is high in temperate species (Makepeace & Patterson, 1980), however much less is known about these interactions for subtropical species (Martin, 1996).

Studies of the effects of ENSO on insular birds are mostly restricted to seabirds, and to influences on demography (survival and breeding success) (Bunce et al., 2002; Barbraud & Weimerskirch, 2003; Smithers et al., 2003; Chambers et al., 2011); less attention has been given to the impacts on insular terrestrial birds. The avifauna of the Galapágos provide the best exemplars of the impacts of ENSO events on insular terrestrial passerines, where it has been linked to breeding success and even rapid phenotypic change (Gibbs & Grant, 1987; Grant & Grant, 1987a; Grant et al., 2000). On arid islands, such as the Galapágos, ENSO events and specifically rainfall trigger dramatic increases in population size of passerine species (Grant et al., 2000).

Indices of large-scale climate patterns, such as ENSO and NAO (North Atlantic Oscillation), are commonly used to assess the impact of climate variation on

population dynamics (Post & Forchhammer, 2002; Stenseth et al., 2003; Sandvik et al., 2005) and in some cases are argued to be better predictors of demographic rates than local scale climate measures (Hallett et al., 2004). However, these indices simplify a sum of climate components (e.g. rainfall, temperature, winds) acting over very large geographical areas, where in their place local climate measures may be better predictors of local demographics. Thus, it is important to identify which climate variable is the most appropriate.

In this study, we evaluate the influence of climatic factors (ENSO and rainfall) and population density on the survival of an insular population of a silvereye subspecies (*Zosterops lateralis chlorocephalus*). We used mark-recapture techniques to analyse a 15-year dataset of a small, closed population, restricted to Heron Island, Australia. We assess the influence of climatic variation using variables summarizing climate at both broad and local geographic scales, as well as the influence of population density on the survival probabilities among seasons across three silvereye age classes. This study will contribute to the understanding of the impacts of environmental factors during different stages of the life cycle of insular birds in the less studied subtropical areas.

Methods

Study site and species

Heron Island (23^{o} 26' S, 151^{o} 57' E) is a wooded island of the Capricorn-Bunker Group, covering an area of approximately 17 ha, located 70km from the eastern Australian Coast on the southern Great Barrier Reef. Mean annual rainfall is 1027.8 mm (1956-2007), and mean max and min temperatures are 26.2 ˚C and

20.8 °C (1962-2007), respectively (Australian Bureau of Meteorology, www.bom.gov.au). The Capricorn silvereye (*Zosterops lateralis chlorocephalus*) is the only regularly breeding passerine on the island (Kikkawa, 1976); it is a long-lived species, reaching ages of up to 16 years; juveniles reach breeding age in the summer the year after hatching (Kikkawa, 1980b). Individuals within the population have been colour-banded since 1964 and survival and fecundity were monitored in detail from 1979 to 1993 (Kikkawa, 1977), under the ethics approval from the University of Queensland. The breeding population size varies between 250 and 500 individuals (McCallum et al., 2000b). Active searches for nests were conducted throughout the island during the breeding season and nests were subsequently monitored until the last nestling fledged. The number of eggs that hatched in each nest was counted, as well as the number of nestlings that fledged (Kikkawa & Wilson, 1983). Description of the species and details of field methods during the study period are given in (Kikkawa, 1980b; Catterall et al., 1982; Kikkawa & Wilson, 1983). Between 1980 and 1993 the percentage of un-banded birds in the population ranged between 0.3% and 4.2% (one to 16 individuals)(McCallum et al., 2000b), while movement among the islands of the Capricorn-Bunker Island Group is estimated to be <1% per generation, making the population effectively closed (Kikkawa & Wilson, 1983).

Capture histories

Capture-recapture (CR) history data were obtained from individually colour-banded birds captured and resighted (recaptured) between 1979 and 1993, constituting a dataset of 60 time-steps. Each time step represents a season,

corresponding to spring (September), summer (October-January), autumn (February-March) and winter (May-July). Although bird censuses were usually made during the same months each year, frequency of visits meant that on some occasions sampling months varied between years: birds were censused in all four seasons most years, but no resighting censuses were conducted during spring 1979, spring 1980, autumn 1981, autumn 1982 and winter 1993. Most birds were first captured as nestlings, and the remainder as juveniles and adults. All nestlings were first captured during summer; juveniles in summer, autumn or winter; and the remaining birds as adults throughout the year. Because nestlings transition to juveniles within the summer season (nestlings fledge at 10-12 days)(Catterall et al., 1982), they violate the CR model assumption that individuals transition age classes between time-steps, not within them (Lebreton et al., 1992). Therefore, nestling survival was analysed using a generalized linear model approach (n=6194), described below.

A capture history dataset was created for all nestlings that survived to juvenile stage, and individuals first captured as juveniles or adults (n=4345). The first capture occasion of nestlings was suppressed in the capture history and was reclassified to the new age class according to the season in which they were first resighted (i.e. summer, autumn and winter of hatch year were reclassified as juvenile; next spring and onwards as adult). Birds that were first banded as nestlings, but that were not resighted as independent birds were removed from the capture history dataset (n=2530) - those individuals were still considered in the nestling models. All juveniles were considered to transition to the adult age in their first spring after hatching; they remained as adults until death. The number of juveniles born and captured during their first-year spring was too low

(n=39) to test this season for juveniles as a variable in the models. Thus, only summer, autumn and winter were included for juveniles.

Environmental covariates

To test the effects of environmental variation on apparent survival we selected a broad scale climate covariate, the Southern Oscillation Index (SOI) and rainfall as a local scale weather covariate. The SOI measures the oscillation in surface air pressure between the tropical eastern and western Pacific Ocean waters and influences broad scale weather patterns in the Pacific (Stenseth et al., 2003). The SOI has been shown to influence population dynamics of a wide range of species (Gibbs & Grant, 1987; Grant & Grant, 1993; Jaksic et al., 1997; Lima et al., 1999; Jaksic, 2004; Holmgren et al., 2006; Oro et al., 2010). Rainfall recorded on the island was used as the local scale weather covariate. For silvereyes on Heron Island, moderate rainfall has been associated with good food supply, but causes nest failure when high (Catterall et al., 1982), as well as high adult and first year mortality in extreme weather events, like cyclones, when intense rainfall is accompanied by strong winds (Brook & Kikkawa, 1998; McCallum et al., 2000b). The effect of cyclones was not included in the analysis due to a low recurrence of these events, where only two cyclones impacted the island during the study period, from which the population recovered rapidly in both occasions (McCallum et al., 2000b). For nestlings, we used the monthly SOI value of the month in which the nestling hatched, while for rainfall we calculated the mean rainfall over the 12-day nestling period (Rain12) for each nest, starting from hatch day. To test for the importance of rainfall earlier and later in the nest occupancy period, we also calculated mean

rainfall for the first and last six days (RainF6 and RainL6, respectively). For juveniles and adults, monthly SOI values were averaged over three-month census periods. Daily rainfall values were averaged over three-month census periods, from now on referred to as seasonal rainfall (SR). To assess if SR has a lagged effect on food supply and hence survival, we added a one-month lag to the three-month rainfall averages, as well as a one-month lagged SOI effect. SOI and rainfall data were obtained from the Australian Bureau of Meteorology (www.bom.gov.au). We were unable to include temperature as a covariate in the analysis due to a large gap in the dataset of the Australian Bureau of Meteorology that completely overlapped with our study period. To test for an effect of the time of the breeding season in which nestling hatched, we assigned a number to each nest from the earliest nest hatch date to the latest according to the breeding season in which that nest was found.

Density

Density was calculated as the total number of juveniles and adults resighted during each season. Nestlings were not included because we assumed they were not strong competitors, being dependent upon their parents, and would not influence survival or recapture rates of independent birds.

Nestling survival analysis

The nestling period is temporally different to juvenile and adult age classes and was thus analysed separately. We constructed generalized mixed linear models (GLMMs) in the package lme4 (Bates et al., 2015) with a binomial error structure in R (R Core Team 2015), with one of two binomial response variables

– the number of nestlings that survived to day 8 when they were banded (n=4122) versus number that hatched (n=6194), and number of nestlings that fledged (n=3922) versus number that hatched (n=6194). We included combinations of 10 fixed effects in each model: mean 12-day rainfall (Rain12), mean rainfall of first six nest days (RainF6), mean rainfall of last six nest days (RainL6), SOI, hatch date, quadratic effect of Rain12, quadratic effects of RainF6 and RainL6, quadratic effect of SOI and population density. Two random effects were also included, year, and pair identity (Pair ID), since the same pair could have multiple clutches in one breeding season. Model selection was conducted by first building two alternate full models and then excluding variables one at a time. Model 1 included all variables except for RainF6 and RainL6; the other included all variables except for Rain12 (Model 2). Thus, the two models were as follows:

Model 1:

$$\text{Probability of Survival} \sim \text{Rain12} + \text{Rain12}^2 + \text{SOI} + \text{SOI}^2 + \text{Hatch Date} + \text{Density} + (1|\text{Year}) + (1|\text{Pair ID})$$

Model 2:

$$\text{Probability of Survival} \sim \text{RainF6} + \text{RainF6}^2 + \text{RainL6} + \text{RainL6}^2 + \text{SOI} + \text{SOI}^2 + \text{Hatch Date} + \text{Density} + (1|\text{Year}) + (1|\text{Pair ID})$$

Models were ranked using Akaike's Information Criterion (AIC), considering a ΔAIC > than two, to identify the model of best fit (Burnham & Anderson, 2002).

Juvenile and adult survival analysis

For juvenile and adult CR data, goodness of fit tests (GOF) were performed in the program U-CARE (Choquet et al., 2009). We found a lack of fit due to a "transience" effect in juveniles (1.798, p=0.036), and in adults (8.351, p=5.551e-017). Due to the closed nature of our study system, transient individuals are extremely unlikely; and the effect we detected was most likely due to juvenile transition to the adult age class, rather than the movement of juveniles off the island. Thus, we account for the transition between juvenile and adult age classes by maintaining an age class effect in every model. The trap dependence test showed a significant "trap-happiness" effect (juveniles: -3.692, p=0.0002; adults: -9.527, p=0), where trapped individuals are more likely to be trapped again than un-trapped individuals. We accounted for this by incorporating a trap-awareness transition matrix to the model, which treats individuals as having a trap response immediately after being trapped but reverting to a naïve state if not recaptured the next trapping session (Pradel & Sanz-Aguilar, 2012) (S1A, S1B and S1C Tables).

We developed a single-state CR model, where individuals were observed or not observed at each time step. We analyzed 4,345 individual CR histories to estimate survival probabilities across seasons using standard CR statistical analysis (Lebreton et al., 1992) implemented in the program E-SURGE (Choquet & Nogue, 2010). CR methods explicitly take into account the probability of an individual being alive but not recaptured by modeling survival

and recapture probabilities simultaneously (Lebreton et al., 1992). They are also flexible, allowing assessment of covariates on the variation of recapture and survival rates over time. All the environmental covariates and density values were rescaled to have a mean of zero and standard deviation of one. Model selection was conducted by first testing if survival and detection rates were constant or varied among seasons. Because the recapture rate was below one and varied between years, we investigated which recapture model best fit our data. Recapture models considered yearly, seasonal and age variation, as well as additive effects of density, SOI and SR. We then built survival models accounting for yearly, season and age variation, as well as linear and quadratic effects of the environmental covariates, and tested them simultaneously with our optimal recapture model. The time to achieve model fit was considerable due to the number of parameters being estimated for variation between every time-step and age; hence we grouped time-steps into seasons across all years. From our base model of season by age we then approached model selection by considering single, additive and interaction effects among the environmental and density covariates. Models were ranked using AIC values, considering a ΔAIC of two, to identify the model of best fit (Burnham & Anderson, 2002). Finally, we extracted the covariate parameter estimates from the model of best fit, which indicated the strength and direction of the relationships of each covariate with survival and recapture.

Results

Nestling survival

Model selection revealed the best-fit model included additive fixed effects of Rain12, SOI, hatch date, density and random effects of year and pair ID on survival. Survival was negatively associated with Rain12 during the nestling period (Table 1), meaning that as rainfall increased nestling survival decreased. SOI was positively related to survival, meaning that survival was higher when El Niño cycles were weaker. Hatch date was positively related to survival, thus survival increased with hatch date, indicating that the later hatching occurs, the high survival probability the chick will have. Density was negatively related to survival, meaning that nestling survival decreased as density of juveniles and adults on the island increased.

Table 1. Parameter estimates for the best-fit model of nestling survival with standard error.

	Rain12	SOI	Hatch Date	Density
Effect Size	-0.18 ± 0.03	0.12 ± 0.05	0.19 ± 0.04	-0.32 ± 0.08

Treating Rain12 as two variables, corresponding to mean rainfall in the first and second half of the nesting period (RainF6 and RainL6) did not produce a better-supported model compared to treating mean rainfall across the nesting period as a single variable. However, in the model that did include these two rainfall variables, the effect of rainfall during the first six days was significant (-0.11; p=0.002), while that in the last six days it was not (-0.03; p=0.459). Survival decreased with rainfall over the first six days, and was virtually constant for the

remaining six days. This could be explained by a quadratic effect of rainfall. However, the model including a quadratic effect of rainfall was not statistically supported, possibly because it removes a degree of freedom. The list of models can be found in the S2 Table.

Juvenile and adult survival

The survival model of best fit included an interaction between season and age, density and age, additive effects of density, SOI and SR and an interaction between density and SR (S3 Table). Survival varied among seasons and between age classes (Table 2). Juvenile survival was high during summer and decreased during autumn and winter. Adults had a higher survival rate overall, compared to juveniles (0.81 and 0.59, respectively), the highest being 0.93 in spring, 0.88 in summer, 0.91 in autumn, and declining to 0.78 over winter (Fig 1). The overall recapture probability for juveniles was 0.39 and for adults was 0.63.

Table 2. Parameter estimates from best-fit model for Juveniles and Adults Survival, with standard error.

	Spring	Summer	Autumn	Winter
Juvenile survival	-	0.96 ± 0.29	0.76 ± 0.07	0.63 ± 0.06
Adult survival	0.93 ± 0.06	0.88 ± 0.06	0.91 ± 0.11	0.78 ± 0.04
Recapture rate	0.19	0.60	0.42	0.46

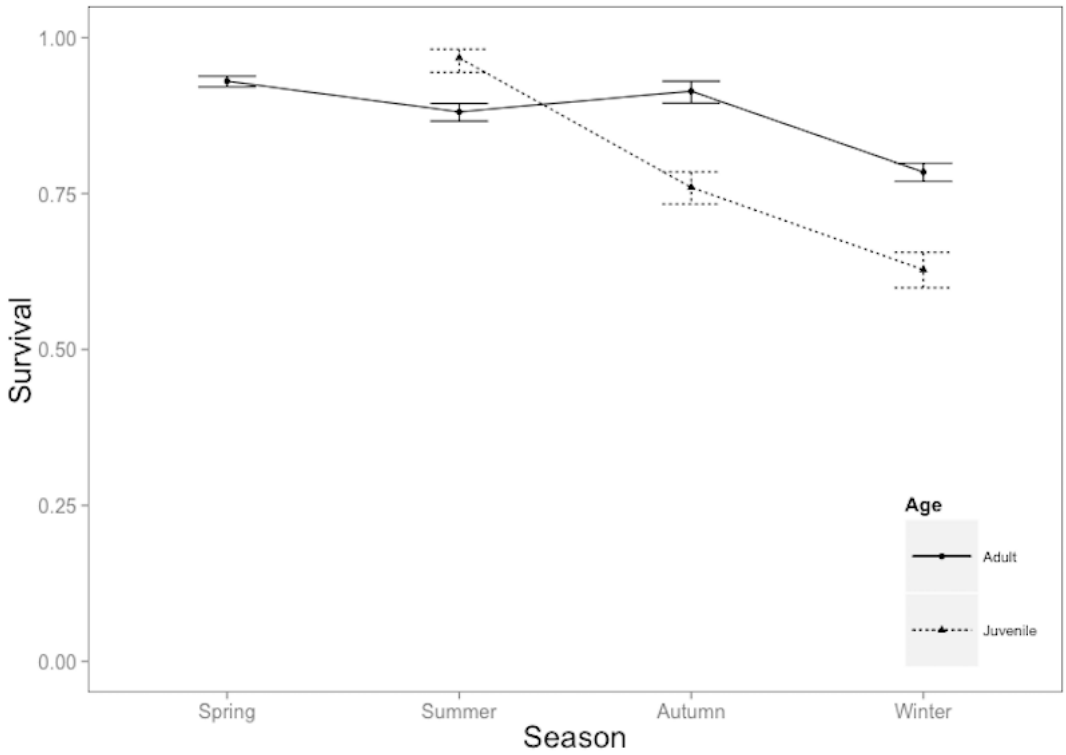


Fig 1. Survival estimates from best-fit model (Season x Age + N + N x Age + SOI + SR + N x SR) for juveniles (white circles) and adults (black circles) across seasons.

In the best-fit model, density, SOI and SR all showed a negative effect on survival (-3.08, -0.11, -0.38, respectively), while the interaction between density and SR was positive (0.56). Survival was highest at times of low density and low SR (Fig 2).

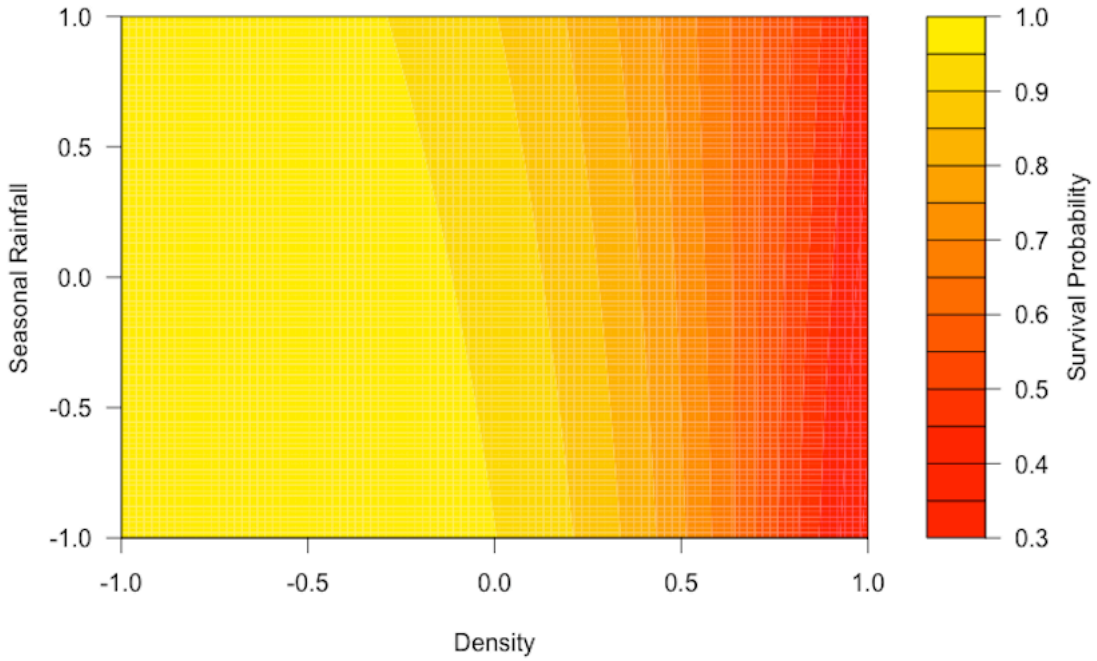


Fig 2. Interaction plot between standardized density and SR in the best-fit model of juvenile and adult survival. The colour scale represents survival probabilities, high values in the colour scale (yellows) represent high survival probabilities and low values in the colour scale (reds) represent low survival probabilities. At lower densities and mean rainfall, survival estimates are higher (light yellow), high density results in lower survival estimates (dark red) and survival decreases slightly as rainfall increases at mid and high densities.

Discussion

This study demonstrates that climatic fluctuations and population density are key factors affecting survival in an insular passerine, where the local scale climate explained survival across all age classes the best. For nestlings, the direct impact of rainfall, SOI, hatching date and density were important factors influencing survival. For adults and juveniles, years of higher rainfall were detrimental to survival when density was also high, suggesting a climate-density interaction.

Survival probabilities were high both for juveniles and adults, as expected for subtropical passerines (Martin, 1996; Johnston et al., 1997). Our results concord with survival estimates obtained by Clegg et al. 2008 (Clegg et al., 2008)from this population in a more recent period (1999-2003), where adults also maintained year-around high survival (0.81) and juvenile survival varied seasonally, with lower survival in winter (~0.40). Our survival estimates on the island are also higher than those previously reported from the mainland (0.61)(Yom-tov et al., 1991). The interaction between rainfall and density for adults and juveniles predicts low survival when both rainfall and density are high, but low survival probabilities when density is at its highest, regardless of the amount of rainfall. Similar findings have been described in seabirds, where poor climatic conditions associated to ENSO interact with density-dependence and decrease survival (Barbraud & Weimerskirch, 2003). Our results are with concordance with a density-dependent population, supporting the results of McCallum et al. (2000) of the same population, were juvenile survival was dependent on adult density.

Rainfall can affect survival directly (e.g. thermoregulation, reduced foraging opportunities or insect activity)(Radford et al., 2001) or indirectly (e.g. lag effect of fruit and/or insect availability)(Bergallo & Magnusson, 1999; Owen-Smith et al., 2005). Our results suggest that rainfall was more likely to be influencing survival directly via thermoregulation of individuals, reduced foraging opportunities during events of harsh weather. Nestling survival would most likely be affected via thermoregulation, since in most passerines nestlings are not able to thermoregulate immediately after hatching, but develop it gradually (Dunn, 1975). This would also explain the significant effect of rainfall during the first six days of the nestling period, but not during the last six days, when we tested the rainfall effect as two variables. Moreover, adults spend more time brooding nestlings (Radford et al., 2001) and less time foraging during rainfall (Poulsen, 1996); this implies that parents are spending less time feeding themselves, as well as their offspring, and could be a factor that explains the SR effect on survival of silvereye adults. Juveniles may be experiencing increased starvation from a combination of the effects of reduced foraging time, decreased insect activity and weak foraging skills (Sullivan, 1989). Additionally, we found no support for an indirect lagged effect of SR; which could be related to increases in food availability after rainfall. This may be due to the lagged variable not accurately matching with food availability or perhaps food resources were not a constraint during the study period. Direct measures of seasonal food availability would allow us to gain insight into its link with rainfall, but such data were unavailable.

Studies on other islands have assessed the demographic impact of food availability on bird populations. Grant et al. (Grant & Grant, 1987b; Grant et al., 2000) showed how heavy rainfall in the Galapagos boosted insect and seed availability, which resulted in drastic increases of fledgling production in two species of finches, altering the size and age class structure of the population. In the Canary Islands, rainfall-mediated food availability influenced the onset of breeding in Stonechats (*Saxicola dacotiae*), but did not significantly alter fledgling success (i.e. nestling survival)(Illera & Diaz, 2006). However, these cases show how rainfall-mediated food availability influences aspects of demography in arid environments, where scarce rainfall is a constraint on food availability (Whitford, 2002). In contrast, our study site is located in a subtropical zone where there are periods of rain throughout the year, and food resources, namely insects and figs, are available year-round (Catterall et al., 1982). On Heron Island, Catterall (Catterall et al., 1982) previously calculated proxies for food availability, in terms of potential food resources across the island, and determined that in areas with higher “fig availability” there was a significantly higher fledging success.

However, the link between rainfall and “fig availability” was not determined. Furthermore, our results did not show evidence of a food-mediated impact on survival through a lagged-rainfall effect. Thus, the specific mechanism by which rainfall and rainfall-mediated food availability impacts nestling survival remains unclear.

In regard to the hatching date, our findings may be in contrast to much of the literature, where nestling or fledgling survival decreases as the breeding season goes on (Perrins, 1965; Verhulst & Tinbergen, 1991; Siikamaki, 1998; Verboven & Visser, 1998; Muller et al., 2005; Arnold et al., 2006; Tarof et al., 2011), albeit most of this literature is from studies that have been conducted in the northern hemisphere. In the southern hemisphere other studies in passerines have reported similar findings, where nestling survival increased slightly as the breeding season progresses (Massoni et al., 2007), attributed to higher likelihood of poor weather early in the breeding season. However, more research is needed to understand the causes and if this pattern is found throughout the southern hemisphere.

High population density was detrimental to nestling survival. Similar findings have been found for birds breeding in the northern hemisphere, where breeding success is density dependent (Alatalo & Lundberg, 1984; Arcese & Smith, 1988; Torok & Toth, 1988). A suggested driver of the density-dependence has been pair competition for food resources. This is one of the likely factors influencing nestling survival at our study site, as it has been previously supported by Catterall et al. 1982 (Catterall et al., 1982), where they found that pairs with territories containing increased access to food resources (measured in number of fig trees per territory) fledged more young. However, they also found that the parents' age and capacity to find insects were important factors in fledging success. Where older parents and those who fed more insects to their nestlings were able to fledge more young.

In recent years the use of large-scale climate pattern indices to study the effects of climatic variation on population dynamics have often proven to be better predictors of ecological processes than weather measured at a local scale (Stenseth et al., 2003; Hallett et al., 2004). The weak support from our models for a role of SOI may be due to a weak relationship between SOI and rainfall in Australia during the study period (Suppiah, 2004). The strength of the relationship between SOI and rainfall in Australia can vary in decadal phases (Suppiah, 2004). This may explain why, even though ENSO events influence rainfall patterns, SOI was not able to explain variation in survival as well as locally measured rainfall. Thus, it remains to be tested if during periods when rainfall and SOI are strongly correlated, SOI would be a better predictor of variation in survival. Nonetheless, it is important to include both local and large-scale climate patterns when modelling the effects of climate on population dynamics in order to not overlook aspects of the relationship.

The frequency of El Niño events is predicted to increase (Timmermann et al., 1999), which would result in dryer conditions in eastern Australia (Allan, 1987). According to our results, less rain would be predicted to have a positive impact on survival across all age classes. Moreover, a previous study on Heron Island showed rainfall to be important in the onset of nesting in silvereyes (Eguchi, 1993), presumably linked to insect and fig availability. Additionally, postponed nesting triggered by less rain could also contribute to higher survival, as our nestling model showed higher survival for nestlings hatched later in the breeding season. However, the long-term effect of lower rainfall on insect and fig abundance on the island is difficult to predict, but would most likely be

negative. The long-term dynamics of the population will depend on the outcome of the positive influences of the predicted lower rainfall on survival and if the effect of lower rainfall on food availability becomes a constraint on survival across age classes.

Our results contribute to our understanding of the population dynamics of subtropical insular passerines, and the links between stochastic environmental and density-dependent effects. In this case rainfall was a key factor, interacting with density, while large-scale climate pattern indexes were unable to explain individual variation in survival at such a local scale. Future studies should incorporate measurements of food availability in the models, to differentiate between direct and indirect effects of climatic variation on survival probabilities.

Acknowledgements

We thank the invaluable contribution of all those that helped in collecting the data used in this paper. A special thanks to J. Massey for sharing his knowledge of capture recapture methods. The study program under which this study was conducted was funded by the Programa de Capital Humano Avanzado scholarship from the Comisión Nacional de Investigación Científica y Tecnológica (CONICYT, Chile).

Supplementary Information

S1A Table. First stage of the transition matrix used in E-SURGE for juvenile and adult models.

	Trap Aware	Trap Unaware	Dead
Trap Aware	y	-	*
Trap Unaware	-	y	*
Dead	-	-	*

S1B Table. Second stage of transition matrix used in E-SURGE for juvenile and adult models.

	Trap Aware	Trap Unaware	Dead
Trap Aware	y	*	-
Trap Unaware	y	*	-
Dead	-	-	*

S1C Table. Event matrix used in E-SURGE for juvenile and adult models.

	'0'	'1'
Trap Aware	-	*
Trap Unaware	*	-
Dead	*	-

For interpretation of these tables please refer to Pradel and Sanz-Aguilar 2012.

S2 Table. Model selection results for GLMMs of nestling survival probabilities and additive fixed and random effects.

Model Structure	AIC	ΔAIC	K
Rain12 + SOI + Hatch Date + Density	**6379.5**	**0**	**7**
Rain12 + $Rain12^2$ + SOI + SOI^2 + Hatch Date + Density	6381.3	1.73	9
Rain12 + Hatch Date + Density	6382.8	3.24	6
Rain12 + SOI + Hatch Date	6392.2	12.59	6
RainF6 + $RainF6^2$ + RainL6 + $RainL6^2$+ SOI + SOI^2 + Hatch Date + Density	6392.4	12.94	11
RainF6 + $RainF6^2$ Hatch Date + Density	6393.4	13.83	7
RainF6 + $RainF6^2$ + RainL6 + $RainL6^2$ Hatch Date + Density	6394.5	15.01	9
RainF6 + RainL6 + Hatch Date + Density	6398.4	18.78	8

For each model, the AIC, the difference in AIC from the best model (ΔAIC) and the number of parameters (K) is provided. The model of best fit is highlighted in bold. Description of fixed effect parameters can be found in the methods. All models include random effects of Year and Pair ID.

S3 Table. Model selection results for survival analysis of juvenile and adult silvereyes.

Model Structure	AIC	ΔAIC	K
Season x Age + N + N x Age + SOI + SR + N x SR	**36054.43**	**0**	**20**
Season x Age + N + N x Age + SOI + SR + N x SOI	36068.95	14.52	20
Season x Age + N + N x Age + SOI + SR	36076.09	21.66	19
Season x Age + N + SOI + SR + N x SR	36077.20	22.77	18
Season x Age + N + N x Age + SR + N x SR	36082.43	28.00	19
Season x Age + N + N x Age + SOI	36088.28	33.85	18
Season x Age +N + SOI + SR	36109.87	55.44	17
Season x Age + N + lagSOI	36109.99	55.56	16
Season x Age + N + N x Age	36114.09	59.66	17
Season x Age + N + SR + NxSR	36123.72	69.29	17
Season x Age + N + SOI +NxSOI	36123.90	69.47	17
Season x Age + N + lagSR	36124.15	69.72	16
Season x Age + N + lagSOI + NxlagSOI	36128.72	74.29	17
Season x Age + N + SR	36144.38	89.95	16
Season x Age + N + SOI + SR + NxSOI	36147.24	92.81	18
Season x Age + SR + SR^2	36149.05	94.62	16
Season x Age + N + lagSR NxlagSR	36172.76	118.33	17
Season x Age + N + SOI	36174.88	120.45	16
Season x Age + lagSOI	36180.74	126.31	15
Season x Age + N + SOI + SR+ lagSR	36189.22	134.79	18
Season x Age	36212.09	157.66	14
Season x Age + SOI	36274.81	220.38	15
Season x Age + SR	36291.79	237.36	15
Season x Age + N	36592.32	537.89	15
Season x Age + lagSR	36857.51	803.08	15
Season x Age + SOI + SOI^2	37125.35	1070.92	18
Intercept	39325.16	3270.73	3

For each model, the AIC, the difference in AIC from the best model (ΔAIC) and the number of parameters (K) is provided. The model of best fit is highlighted in bold. “Season” denotes a seasonal effect, “Age” an effect of juvenile versus adult age classes, “N” a density effect, “SOI” a three month mean Southern Oscillation Index (SOI) effect, “lagSOI” a one-season lag SOI effect, “SR” a three month mean seasonal rainfall effect, and “lagSR” a one-season lag seasonal rainfall effect.

CHAPTER FIVE

Life history variation and insular body size in birds: an approach using integral projection models

Erik M. Sandvig & Tim Coulson

Abstract

The novel environmental conditions species experience following the colonisation of island are known to generate a series of convergent adaptations. Among these insular adaptations are changes in morphology and life history. In birds, one of these morphological changes is that of large-bodied species evolving to smaller body sizes on islands and smaller species becoming larger, termed the ‘island rule’. However, the mechanisms underlying this pattern remain unclear. Additionally, slower life histories strategies are adopted in insular environments, and are generally thought to be fundamentally linked with body size. In this study I investigate the links between life history traits and body size in an insular passerine population using an integral projection model approach. I found that the model predicts the optimal pathway to increase the average body size of the population is to grow faster during development and that slowing growth would have demographic costs. However, small-bodied birds that undergo body size increases on islands tend to grow more slowly. These results suggest that for island birds that are larger than their mainland ancestors there are constraints to faster growth or that there are benefits to growing slower that outweigh those of faster growth.

Introduction

Insular environments are an interesting system to study life history adaptations, as island populations are exposed to a predictable set of conditions that differ from their mainland counterparts (Grant, 1998b; Blondel, 2000; Losos & Ricklefs, 2009; Weigelt et al., 2013). Of the characteristics of insular environments, low predation pressure and high intraspecific competition are often attributed to be important drivers underlying a suite of recurrent insular adaptations termed the 'insular syndrome' (Covas, 2016). In birds, this has been shown in shifts towards slower life history strategies (Covas, 2012) and changes in body size (Clegg et al., 2002), among changes in demography, behaviour, colouration and immune resistance (Adler & Levins, 1994; Blondel, 2000; Doutrelant et al., 2016; Loiseau et al., 2017). Island birds lay smaller clutches, have longer nestling periods, grow more slowly, and have higher survival (Bosque & Bosque, 1995; Covas, 2012, Sandvig et al. in prep). Body size patterns on islands show large-bodied species becoming smaller on islands and small species becoming larger, referred to as the 'island rule'. Body size changes are fundamentally linked to life history adaptations, as the body size of an individual is determined by developmental processes.

Life history traits describe the key patterns of growth, maturation, reproduction and survival of organisms. Life history theory traditionally works under the assumption that body size is a key determinant of individual fitness (Roff, 1992; Stearns, 1992), with survivorship and reproductive schedules changing with adult body size. Life history strategies are often thought to arise from trade-offs between the reproductive benefits of size and the costs of longer growth

periods prior to reproduction commencing (e.g. mortality risk). The study of the impacts of environmental change on variation in life history traits can give us insights into the mechanisms producing phenotypic change (Flatt & Heyland, 2011), as well as the demographic effects produced by changes in survival and reproduction (Saether & Bakke, 2000). Understanding the relationships and interactions between survivorship and reproductive schedules and body size is key to understanding the mechanisms behind insular body size evolution.

Understanding the links between insular body size and life history changes requires tracking body size and life history traits simultaneously. Integral projection models (IPM) provide a framework to do this, by capturing the dynamics of continuous phenotypic traits such as body size and tracking the association of this trait with life history traits over time (Coulson, 2012). The functions describing these relationships can be further broken down to describe how they vary across age (Ozgul et al., 2010), providing insights into the interactions at different stages of the life cycle. IPMs can be parameterized using data commonly collected in long-term mark-recapture studies (Merow et al., 2014; Rees et al., 2014) and offers the potential to simultaneously investigate the phenotypic and demographic consequences of life history changes.

In this study we use a structured modelling framework to address questions of the role of life-history shifts in the body size and population dynamics of an insular environment. We parameterise the model using long-term data for three age classes from a silvereye population on Heron Island, Australia. Body size in

this population is known to divergence significantly from its mainland ancestors, increasing by 40%, and represents an ideal system to investigate body size and life history dynamics of an insular bird. This population lives at high population densities (McCallum et al., 2000b), individuals engage in frequent agonistic interactions (Kikkawa & Wilson, 2002) and they also establish dominance hierarchies where larger size is positively associated with high over-winter survival in juveniles (Robinson-Wolrath & Owens, 2003). Predation is virtually non-existent (Catterall et al., 1982) and food availability during winter appears to be a constraint on juveniles and adults (Clegg et al., 2008). We construct an IPM for this population to pose three specific questions:

1. How does mean body size of the population respond to changes in the life history traits: survival, development, recruitment and inheritance?
2. What are the consequences of life-history changes on the population growth rate?
3. What are the costs or benefits of differing development patterns to population growth rate?

Methods

Model description

The model we use here is an ecological integral projection model that is constructed for body size using four fundamental functions; survival (S), development (D), recruitment (R), and inheritance (H) (Easterling et al., 2000). These functions describe the survival of individuals from one year to the next, the change in mass in grams for individuals that survive, the number of individuals that recruit into the population next year, and the mass of recruits.

The equation for the standard IPM is given below (Equation 1), where Z is the trait at time t, Z' is the trait at time $t+1$, (Z,t) is the distribution of the trait at time t, $N(Z',t+1)$is the distribution of the trait time $t+1$. $Sa(Z,t),\ Da(Z'|Z,t),\ Sj(Z'',t),\ Dj(Z'''|Z'',t),\ Sn(Z',t),\ Dn(Z''|Z',t),\ R(Z,t),\ H(Z'|Z,t)$ are the survival and development functions for adults, juveniles and nestlings, recruitment and inheritance conditional on mass in grams. The survival and development functions were split into three age classes to account for the variation in these life history traits across the life cycle.

Equation 1:

$$N(Z',t+1) = \int [\,Sa(Z,t)Da(Z'|Z,t)$$

$$+ Dj(Z'''|Z'',t)Sj(Z'',t)Dn(Z''|Z',t)Sn(Z',t)H\left(Z'\middle|Z,t\right)R(Z,t)]N(Z,t)dZ$$

Fundamental functions

Survival describes the probability of an individual with a given Z value surviving from time t to $t+1$. The survival function is modelled as a logistic (Equation 2), where $S(Z,t)$ is the probability of survival to $t+1$ for a given value of Z. ß$_0$ is the intercept of a linear regression taking into account effects of Z, ß$_1$ is the slope of the relationship between Z and survival, z_1 is the Z value at t. The three survival functions separated into adults, juveniles and nestlings all have the same form as Equation 2. The intercept for the adult and juvenile models were averaged over all years of data.

Equation 2:

$$S(Z,t) = \frac{1}{1+e^{(-\beta_0+\beta_1 z_1)}}$$

Recruitment describes the number of offspring that survive to recruit into the population at time $t+1$ given the Z value of the mother at time t. In silvereyes juveniles are sexually mature in the year following hatching (Catterall et al., 1982) and can recruit into the population. We use a female only model and assume a pre-breeding census (Rees et al., 2014). The recruitment function takes an exponential form, Equation 3, where α_0 represents the intercept and α_1 the slope of the relationship of Z and recruitment.

Equation 3:

$$R(Z,t) = e^{\alpha_0+\alpha_1 z_1}$$

Development describes the change in a given Z value from t to $t+1$ and inheritance describes the change in a Z' value from the mother's Z value at time t to the offspring Z' value at time $t+1$. Both the development and inheritance functions can be described with Gaussian probability functions of the expected values of Z' at *t*+1 (Z') given Z at time t. These functions contain two components – a linear predictor of the mean of the probability function, and a linear predictor of the variance of the probability function. Firstly, the expected value of Z' given Z at time t is approximated using a linear regression following the same linear predictor form as Equation 3. Second, the standard deviation around these linear relationships is calculated. These two elements can then be combined into Equation 4 to create the Gaussian probability distribution, where the linear predictor generates the expected value of Z' and $SD(Z',t)$ is the standard deviation around Z'. This equation assumes that the distribution of possible Z' values at $t+1$ is normally distributed for any value of Z at t. Inheritance follows the same form but with $H(Z'|Z,t)$ and $H(Z,t)$.

Equation 4:

$$D(Z'|Z,t) = \frac{1}{SD(Z',t)\sqrt{2\pi}} e^{\frac{(Z'-(\alpha_0+\alpha_1 z_1))^2}{2SD(Z',t)^2}}$$

Study system and data collection

Long-term data were collected between 1979 and 2016 through population census of colour-marked individuals during breeding seasons on Heron Island. During each census the island was repeatedly surveyed to record as many

sightings of previously marked birds. Unmarked birds were captured and fitted with a unique metal band and colour combination and aged, sexed and morphometric data collected (detailed description of the census methods can be found in Kikkawa, 1980). During the time period considered for the survival analysis the proportion of the population that remained unmarked ranged between 0.3 and 4.2% (McCallum et al., 2000b). Breeding data were collected by identifying pairs and monitoring their breeding activities from nest-building through fledging; brood size, number of nestlings that fledged and morphometric data at fledging were recorded. During the breeding seasons between 2015-2016 nestlings were measured on day 2 after hatching and day 8 (shortly before fledging) to estimate development at the nestling stage.

Statistical analysis and function parameterisation

Survival

The survival component of the IPM was split into three separate functions describing the relationship between survival and body size at the nestling, juvenile and adult stages. For adults and juveniles, we built capture histories from a subset of the data (1979 to 1994) with continuous breeding survey efforts spanning September of one year to February or March of the next year (N adults = 586, N juveniles = 1373). Individuals were considered to survive to the next year when resighted in the next breeding season. We used generalized linear models (GLM) with a binomial error structure, using the 'lme4' package (Bates et al., 2015) in R, to estimate the probability of survival to $t + 1$ given a value of Z at time t. The response variable was indicated as a 1 if the individual was resighted in the breeding season following the year it was measured or a 0

if it was not. The explanatory variable was the mass in grams of the individuals measured at time t. Because this method does not account for the recapture probability the estimated intercept for adult survival was divided by the adult recapture rate estimated in Chapter 4 to achieve a more representative baseline survival rate. For survival of nestlings within the nest we used a subset of the data from 2015-2016 (N=131). We used a binomial GLM with the response variable indicating if the individual survived until day 8 after hatching (silvereye nestlings fledge between day 11 and 15 after hatching, pers. comm.) and the explanatory variable indicating the mass at day 2 after hatching. We considered there to be a significant relationship when $p < 0.05$ and checked for assumptions of normality in all functions.

Development

The development component of the IPM was split into three separate functions describing the change in weight from time t to $t + 1$ for nestling, juvenile and adult stages. For adults we used data from 2012 to 2014 (N=39) where individuals measured as adults were recaptured and measured the next year. Because of small sample size of individuals measured as juveniles and again as adults, we used long-term data of great tits (*Parus major*) from Wytham Woods as a proxy (N = 5014). We used great tit data because they are of a similar body size to silvereyes and have similar growth rates during the nestling stage (k = 0.413 and k = 0.460, from Barba, Gil-Delgado, & Monrós, 1993 and Chapter 3, respectively). For nestlings we used data from 2015-2016 (N=89) where nestlings were measured on day 2 after hatching and again on day 8 (see Chapter 3 for methods on data collection). For each of these three

functions we fit the data to a linear regression with the first measurement of the individual as the response variable and the second measurement as the explanatory variable. For juveniles the intercept estimate using the great tit data was then scaled from the mean great tit size to the mean silvereye size, leaving the slope the same.

Recruitment

The recruitment function was fit using a GLM with a Poisson error structure with the number of nestlings that survived to recruit into the population at time $t + 1$ as the response variable and the body size of the mother as the explanatory variable.

Broad sense inheritance

Inheritance was calculated using a linear regression between the body size at day 2 of nestlings that recruit into the population the following year and the body size of the mother at time t. We used data from 1992 to 1994 (N=97).

Model construction

We capture the statistical functions in matrix form and combine them into a IPM according to Equation 1. We discretise the IPM by numerical integration methods (Easterling et al., 2000). In this case we use 100 mesh points (cell centres) on an evenly spaced grid describing the size distribution of the population. The lower limit for integration was determined by multiplying the smallest nestling size by 0.9 and the upper limit by multiplying the largest adult by 1.1.

Perturbation analysis of the drivers of population and body size dynamics

To determine the key drivers of the demographic and body size dynamics of the population we assessed the sensitivity of $\bar{Z}$, the mean body size, and the population growth rate to changes in parameters in the fundamental functions. Each parameter was independently perturbed by multiplying the estimate by 1.01 when the number was positive and 0.99 when the number was negative. One parameter was manipulated at a time, leaving all other parameters unchanged. For each manipulation we constructed an IPM where the resulting $\bar{Z}$ and population growth rate were calculated by obtaining the eigenvectors and eigenvalues of the IPM matrix. To calculate $\bar{Z}$ we obtain the stable age structure of the population from the right eigenvector and multiply it by the size distribution of the population and take the sum. The asymptotic population growth rate was obtained from the dominant eigenvalue.

To assess the implications of a range of developmental strategies on population dynamics we assessed the sensitivity of the population growth rate to contrasting changes in the intercepts and slopes of development at different life stages. For each life stage we emulated a range of developmental strategies by setting the intercept at a range of values around the estimated intercept (from 5 to 15 in increments of 1). For each intercept we calculated a corresponding slope such that the line it described intersected a line of intercept 0 and slope 1 at the same point as the original regression, as seen in Figure 1. This was done for each life stage with the estimated parameters of its corresponding development function. When the intercept decreases and the slope is increased it represents slower development and increases in the intercept and decreasing

the slope represents faster development. For each life stage we then constructed IPMs with the manipulated intercept and corresponding slope and calculated the resulting population growth rate.

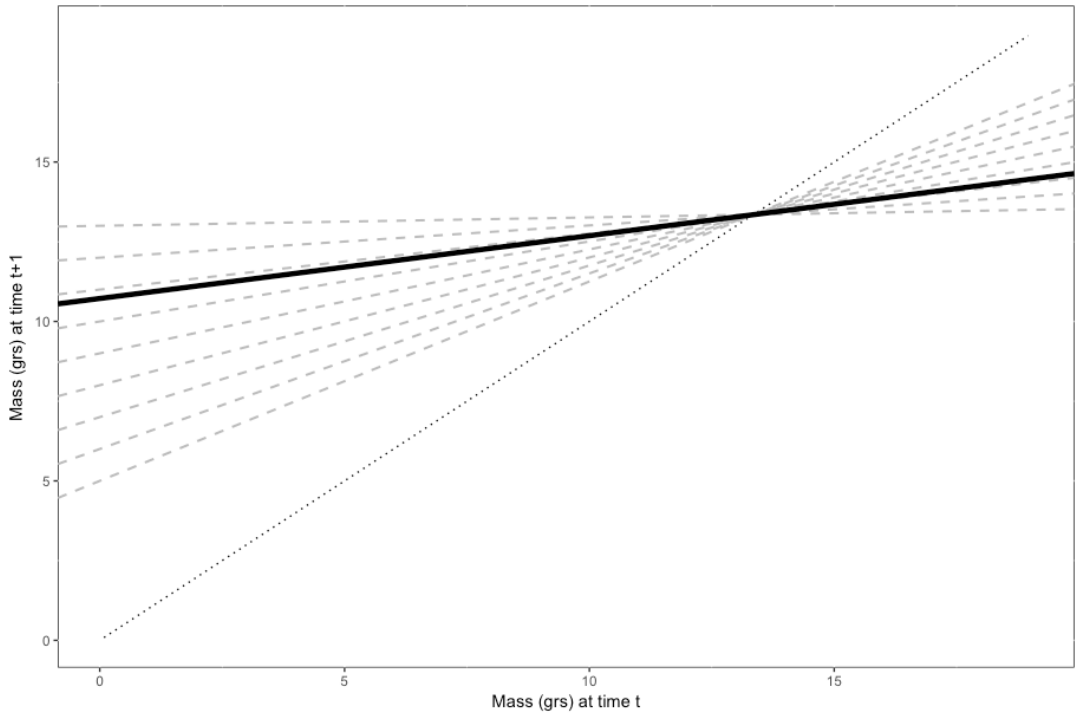


Figure 1. Visualization of development functions tested in perturbation analysis of the effect of developmental strategies on population growth rate. Solid line represent relationship calculated from data, dashed lines represent simulated relationships. The figure depicts the development relationship in adults, the respective development relationship was used for each age class in the model. The probabilities of mass changes from time t and $t + 1$ are given by the size distribution of each age glass. Thus, the probability of changes from 1 to 11 in adults are near 0, because there are no adults that weigh 1 gr in the population.

Results

Statistical analysis and fundamental functions

Results for the fitted models are presented below, showing the intercept and slope for each relationship used in the IPM (Table 1). The stable population growth rate obtained from the dominant eigenvalue was 1.327.

Table 1. Parameter value estimates for fundamental functions. Parameter names follow notations used in Equation 1. SE and p value for juvenile development intercept is not given because the estimate was scaled from great tit mean body size to that of silvereyes.

Parameter	Estimate	SE	p
Sn int	-1.829	0.832	0.03
Sn s	0.869	0.253	<0.001
Sj int	-2.891	0.663	<0.001
Sj s	0.142	0.047	<0.001
Sa int	-0.798	1.018	0.79
Sa s	0.04	0.072	0.58
Dn int	7.694	0.499	<0.001
Dn s	0.632	0.133	<0.001
Dj int	8.683	NA	NA
Dj s	0.361	0.013	<0.001
Da int	10.721	2.897	<0.001
Da s	0.197	0.213	0.36
H int	10.758	0.72	<0.001
H s	-0.015	0.059	0.81
R int	0.507	0.079	<0.001
R s	-0.002	0.006	0.75

Perturbation analyses

The perturbation analysis of the population mean mass showed that $\bar{Z}$ was most sensitive to changes in the development functions (Fig. 2). With increases in the intercept of development of adults and juveniles producing the largest increases in $\bar{Z}$, followed by their slopes and the intercept and slope of nestling development. Increases in the intercept of inheritance also produced increases in $\bar{Z}$.

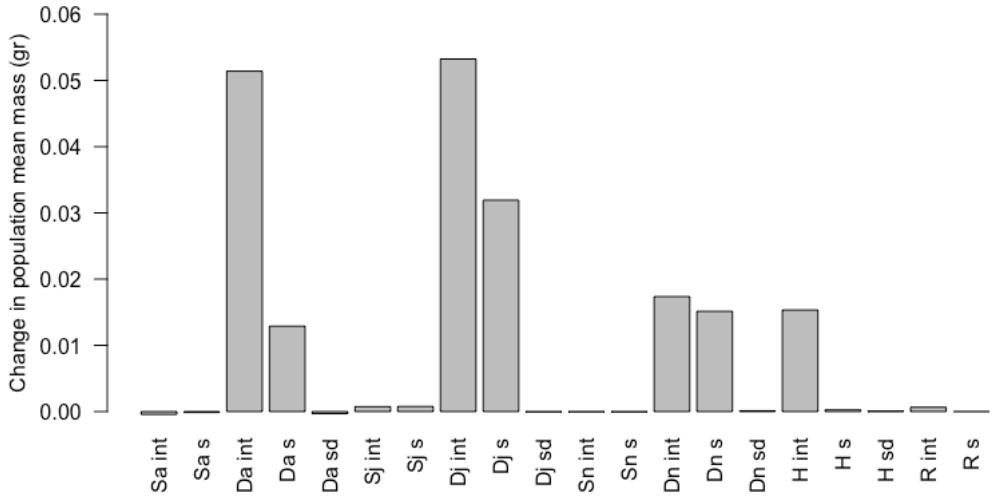


Figure 2. Changes in mean body mass when perturbing the parameters of the fundamental functions.

The perturbation analysis of population growth rate showed that it is sensitive to and increases with changes in the survival functions of adults and juveniles, development in nestlings and the intercepts of inheritance and recruitment (Fig. 3).

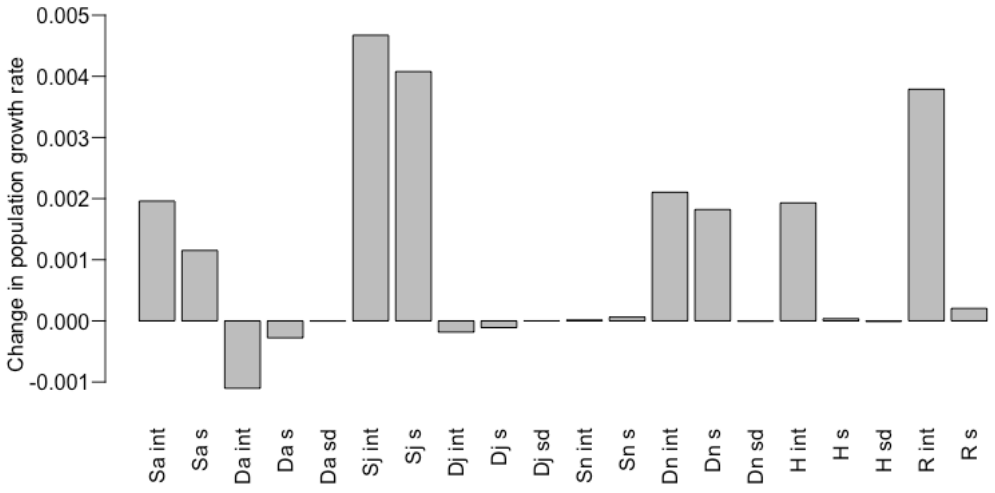


Figure 3. Changes in population growth rate when perturbing the parameters of the fundamental functions.

Decreasing the intercept of and increasing the slope of the development function in nestlings decreased the population growth rate, while increasing the intercept and decreasing the slope produced increases in the population growth rate (Fig. 4). Changes in the development functions of adults and juveniles did not produce noticeable changes in the population growth rate.

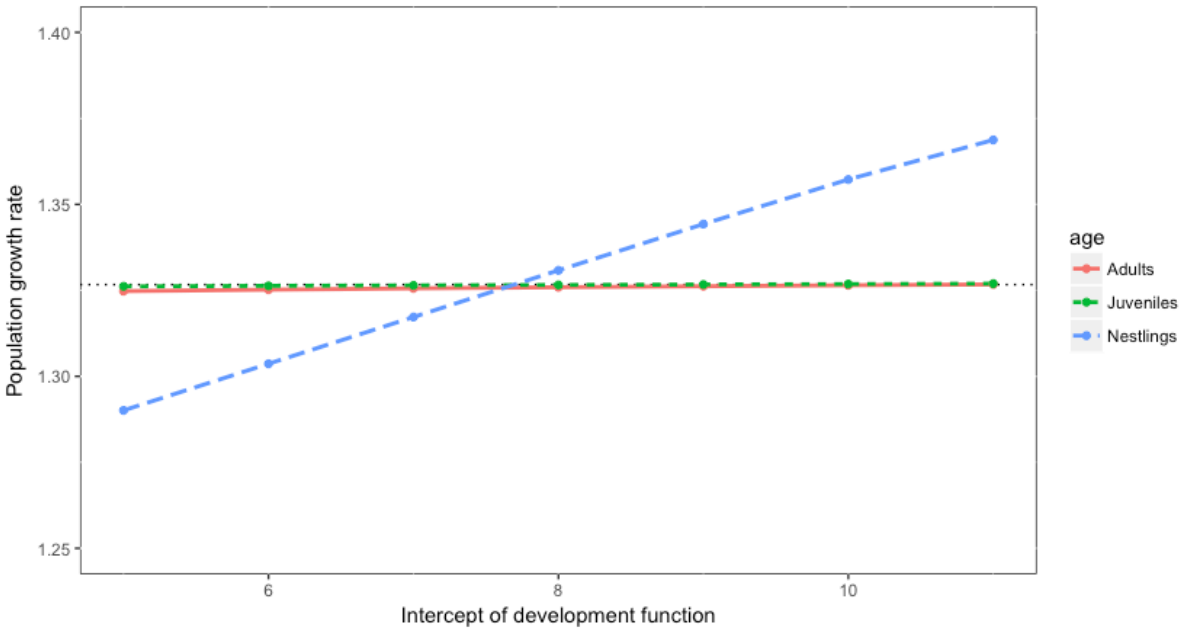


Figure 4. Changes in population growth rate from different developmental strategies. Population growth rates calculated from IPMs with simulated development strategies for adults (black line), juveniles (red line), and nestling (blue line). Dotted black line depicts population growth rate without perturbation.

Discussion

Final model

From the parameterisation of the IPM we can comment on how the life histories in this population are related to body size. The final model captured an influential role of body size on nestling and juvenile survival. These two life stages were found to have lower survival probabilities than adults from earlier analysis (Clegg et al., 2008; Sandvig et al., 2017). Earlier studies have also found juvenile survival to increase with body size and dominance status (Kikkawa, 1980b; Robinson-Wolrath & Owens, 2003). These relationships reflect the importance of body size for individuals in their first year of life in order to survive the winter conditions and recruit into the population. In contrast, the model does not show body size to influence the ability of adults to survive overwinter. Similar findings have been reported previously, where no relationship was found between adult survival and dominance or size (Kikkawa, 1980b). The model captured an effect of body size on the development of nestlings and juveniles, meaning that the larger individuals at the end of these life stages are larger to begin with. No relationship was found for development and body size in adults, meaning that on average adults remain similar sizes from year to year. We did not find an effect of body size on the number or size of recruits either. Thus, body size alone does not predict the number or size of the mother's recruits in this population.

Shifts in growth strategies drive changes in body size

Shifts in body size were predominantly sensitive to changes in the development functions (Fig. 2). This was true for all age classes, for both changes in the

intercept and the slope. When increasing the intercepts and slopes what is effectively happening is that we are increasing the growth rate. Increasing the mass gain between years is equivalent to growing faster. Adults and juveniles have the largest impact on $\bar{Z}$ because they represent a large proportion of the size distribution in the population. It's noteworthy that changes in nestling development impact $\bar{Z}$ because individuals at the nestling stage represent only a small portion of the size distribution. Finally, increases in $\bar{Z}$ from the inheritance function are expected, because increasing the intercept will produce larger offspring for every mother that produces recruits.

What is particularly interesting about the outcome of the perturbation analysis is that it suggests that the optimal pathway to achieve the larger body size in this population is to grow faster. Yet, from the results in previous chapters (Chapter 2 and 3) we have contrasting evidence that suggests that the general development strategy that islands birds adopt is to grow slower. From this we can imply that in this island environments there are either constraints on faster growth, or the fitness benefits of growing slower outweigh those of growing faster, or a combination of both.

Food limitation is thought to be an important driver of within population growth rate variation (Ricklefs, 1976; Searcy et al., 2004; Killpack & Karasov, 2012) and is known to hinder increases in growth rates. On Heron Island there is evidence of seasonal food limitation (Catterall, 1985), where limited resources over winter are thought to explain mortality in juveniles and adults (Kikkawa, 1980b; Clegg et al., 2008) and could be a constraint on growth in juveniles.

However, during the nestling period, when most of the growth of individuals occurs, there is no evidence of food limitation, as seen in Chapter 3. Slower growth in nestlings may be related to a shift in the strategy of resource allocation. Optimization of resource allocation is thought to favour increased survival (Dmitriew, 2011). Consequently, through slower growth it may be possible to produce higher quality offspring. Slower growth can also be beneficial by decreasing oxidative damage during development (Monaghan et al., 2009), which can have detrimental effects on reproductive success and survival. In an environment of high intraspecific competition and released from predation, selection may favour growing slower and for longer if this results in higher quality offspring with higher survival and competitive benefits from increased size. On the other hand, high densities and intense intraspecific competition may limit food availability and constrain growth, particularly for juveniles during the scarce winter months.

Survival and early development drive population growth rate

Population dynamics in long-lived species are predominantly driven by the survival of individuals, over that of reproductive output (Saether & Bakke, 2000). This is what we find for this population where changes in the population growth rate were particularly sensitive to survival of adults and juveniles (Fig. 3). Recruitment has a large effect, because increasing the number of recruits for mothers of all sizes will logically increase the population size, as does increasing the size of these recruits in the inheritance function, as larger nestling have higher survival. Nestling development was found to be important for population growth rate because it's tied into juvenile survival. Increasing the

growth at the nestling stage means larger individuals at the juvenile stage, which would then have higher chances of surviving over winter and recruiting.

Impacts of growth strategies on population dynamics

By changing the growth strategies in adults and juveniles, while maintaining the average body size of the population, there were small changes in the population growth rate. However, growing slower or faster in nestlings produced large changes in the population growth rate (Fig. 4). Shifting to slower growth decreased population growth rate and faster growth increased it. Because this manipulation to the model maintains the average body size of the population, these results highlight an apparent cost of slowing growth in terms of mean fitness. This apparent cost to growing slower at the nestling stage is explained by a larger proportion of nestlings predicted to remaining small, and because nestlings show a strong relationship between survival and size, this model predicts higher nestling mortality and a decrease in population growth rate.

Model limitations

It must be noted that there are many limitations to this model, because it doesn't account for density-dependence in the population, evolution or growth trade-offs. Previous studies have found density-dependence in juvenile and adult survival (McCallum et al., 2000b; Sandvig et al., 2017). The inclusion of density in the model would allow for testing of additional questions of the effect of density on mean body size variation and interactions with life history shifts. Unfortunately, the available data for estimating survival and development functions was not sufficient to capture variation with density.

Conclusions

In this study we have explored the links between life history traits and body size in an insular passerine population. Predictions from the integral projection model show that the optimal pathway to increase the average body size of the population is to grow faster during development and that slowing growth would decrease the population growth rate. However, as seen in Chapter Two, small-bodied birds that are predicted to undergo body size increases on islands tend to grow more slowly, compared to their mainland counterparts. These findings would suggest that there are constraints for faster growth in island birds that have increased in size compared to their mainland ancestors or that there are benefits to growing slower that outweigh those of faster growth. Future studies should try to investigate the roles of food limitation, optimization of resource allocation and dominance hierarchies in the context of insular life history evolution.

CHAPTER SIX

General discussion

This thesis aimed to bring together empirical data on life history and demographic variation and a modelling framework in an island population to better understand the mechanisms behind body size increases as part of the 'insular syndrome'. My work has explored some important topics related to the 'island rule' and the findings of each chapter have increased our understanding of life history and demographic processes in insular environments and highlighted the complexities in developing a holistic understanding of the mechanism behind body size increases on islands.

In Chapter 2, I use a systematically collected dataset to show that small-bodied (<1kg) bird species tend to grow slower on islands compared to mainland populations. This is consistent with the idea that evolution for slowed growth in relaxed insular predation regimes contributes to the pattern of body size increases in small-bodied birds that inhabit islands. In Chapter 3, I use silvereye data to show that there is also a trend toward slower insular growth at the intraspecific level. Growth rates variation within the population is not simply explained by straightforward links with parental size or resource acquisition and more complex processes of resource allocation are likely involved. In Chapter 4, I use a 15-year dataset of individually-marked birds to show that survival probabilities of individuals in the population depend on their age class and time of year. Additionally, all age classes showed density-dependent survival. Moreover, survival probabilities were associated to climatic variation, where

increases in rainfall has detrimental effect on survival for all age classes, and at high densities the negative effect of rainfall was exacerbated. These climatic effects were best detected with measures at the local level. In Chapter 5, I constructed a body size IPM for silvereyes and showed that according to model predictions, faster growth would be the optimal pathway for increasing the population body size and that slower nestling growth would have demographic costs. This suggest constraints on faster growth or fitness benefits to slower growth that outweigh those of faster growth.

Central to the 'island rule' is the principle that body size is regulated by mechanisms that control the length and rate of growth. The process of becoming larger generally involves growing faster (as suggested by the model in Chapter 5) or for longer. Previous studies have shown that insular birds have longer developmental periods (Bosque & Bosque, 1995; Covas, 2012) and in Chapter 2 I have shown that they also tend to grow more slowly. Decreases in growth are usually associated with food limitation, and under a restricted nutrient intake body size would be expected to decrease. However, we see body size increases in an environment that is predicted to be food limited because of high population densities – particularly for overwintering juveniles.

Theoretical and empirical work has shown that growth rates are optimized rather than maximized, and population variation often reflects local adaptation (Shingleton, 2011). Indeed, in Chapter 2 we see that adaptations to insular environments produce a trend towards slower growth in altricial birds. The outcome of growing for longer and at a slower rate on islands is fundamentally

linked to the resource intake during the development period. In Chapter 3 I investigated this process by looking into the links between parental care expenditure and their nestlings' growth rates. Similar to findings by Sofaer et al. (2018), we found that growth rates and parental care expenditure were not directly proportional and concluded that slower growth rates on islands likely involved an optimization of resource allocation that is linked to a prioritization of physiological quality. Slower growth may increase individual quality because faster growth has been shown to have negative effects on individual quality (i.e. survival) (Metcalfe & Monaghan, 2003; Dmitriew, 2011) and growing for longer has been associated to increased survival until independence (Remes & Matysioková, 2016). This may explain the high survival rates we see on islands (Chapter 4) and how they may relate to fitness (Chapter 5).

Previous studies in this population have found juvenile over-winter survival to increase with measures of size (Robinson-Wolrath & Owens, 2003; Clegg et al., 2008). However, the work in Chapter 5 has expanded our understanding of this relationship throughout the life cycle. On Heron Island I found a strong relationship between nestling size and survival until fledging and juvenile survival until reaching breeding age, but no effect on adult survival (Chapter 5). From this it is reasonable to suggest that there is selection favouring larger body size predominantly in the early stages of the life cycle. If an individual passes the selective filters during the nestling stage, large size may then be advantageous if it is associated to behavioural dominance benefits (e.g. successful access to resources that could translate into higher survival). However, the consequences of large body size in adulthood remain unclear, as

to date, a positive relationship between behavioural dominance (i.e. winning agonistic encounters) and reproductive success or survival has not been found (Clegg et al. unpublished; Kikkawa & Wilson, 1983), though the data to test these ideas has been limited in Heron Island silvereyes.

Future directions

In this thesis I have increased our understanding of processes underlying body size evolution on islands. Nevertheless, questions remain and new directions have emerged. There are two primary areas arising from this thesis that I consider to be important to further our understanding of the adaptations we see on islands, particularly relating to the 'island rule'. 1) resource allocation during nestling growth; 2) the role of density-dependence.

To improve our understanding of the mechanisms behind slower growth on islands it would be helpful to investigate the processes involved in resource allocation in nestlings. Under the assumption that growth rates are being optimized for improving individual quality in the context of heightened intraspecific competition we need to know more about the physiological processes driving the growth patterns we see on islands. This includes answers to the following: 1) What are the traits that are prioritized by nestlings during development when predation pressure is relaxed and high intraspecific competition selects for larger size? Determining resource allocation between morphological traits, including internal organs, could help us answer this question. 2) How does intraspecific growth variation and the influence of its drivers differ between island and mainland population? Further intraspecific

comparisons between island and mainland populations, including measures of density and predation risk, could give us greater insights into insular growth rate dynamics. 3) How does increased intraspecific competition in island environments influence variation in nestling growth rates and reproductive success? This question could be addressed by quantifying the influence of the quantity and quality of provisioned food items, including how this is regulated by dominance status, on growth rate variation and reproductive success.

The second area that warrants further research is that of the role played by density-dependence in the 'island rule'. In Chapter 4 we show that survival across age classes was density-dependence, and has been shown previously for adults and juveniles in this population (McCallum et al., 2000b). Experimental studies have shown how density can regulate life histories, such as growth rates (Reznick et al., 2012). Being able to determine how changes in density influence not only survival, but also growth rates and fecundity would allow us to pose questions of how density-dependence is related to body size selection on islands. Extending the IPM developed in Chapter 5 to include the effect of density on the fundamental functions would allow us to address these questions. However, additional data collection would be required to implement this in the silvereye system. Implementing this modelling framework in additional insular systems, that possess adequate data, would be a worthwhile endeavour.

The work developed in this thesis has contributed towards a better understanding of the processes underlying the 'insular syndrome' by identifying

additional insular life history patterns and showing the importance of growth and survival during early life stages for the ‘island rule’. Notwithstanding, there are certainly still questions to be addressed regarding the drivers and mechanisms behind the ‘island rule’ making this an exciting area of study.

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