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Does the 'island rule' apply to birds?

**An analysis of morphological variation between
insular and mainland birds from the Australian,
New Zealand and Antarctic region**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Master of Science (Conservation and Ecology)

at
Lincoln University
by
Elisa Diana Ruiz Ramos

Lincoln University
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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Master of Science (Conservation and Ecology)

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by

Elisa Diana Ruiz Ramos

The 'island rule' states that large animals become smaller and small animals become larger on islands. Morphological shifts on islands have been generalized for all vertebrates as a strategy to better exploit limited resources in constrained areas with low interspecific competition and predation pressures. In the case of birds, most of the studies that validate this rule have focused on passerines, and it is unclear about whether the rule applies to other Orders. Studies suggested insular morphological shift in birds is for greater bill size variation within males and females from the same species, when compared to their mainland counterparts. Increased sexual size dimorphism in island species would represent a strategy for resource exploitation. These insular morphological shifts are thought to be influenced by an island's environmental and physical characteristics. I tested the validity of the 'island rule' within different avian Orders of the Australian, New Zealand and Antarctic region. I compared and analysed existing morphological measurements for insular and mainland related species occurring in the region, linking them with abiotic features of each island using meta-analysis modelling.

Overall, the estimated relative insular body size (i.e., $SR = \text{island size} / \text{mainland size}$) values showed little and inconsistent differences between mainland and insular closely-related bird species using wing, bill, tarsus and weight measurements as predictors of body size. The 'island rule' patterns were partially recognized for bill and tarsus length at the species level, but this weak trend did not prevail at the family or order level. The mean SRs for the assessed traits suggested a minor trend for birds to become larger on islands in spite of the body size of their mainland counterparts. There were no consistent differences between the degree of sexual size dimorphism in islands and mainland species. Island area, distance from mainland, and sea surface temperature were related to small SRs variation. However, because the mean SRs were so close to one, it was not clear if these abiotic

features were important moderators of this ratio. Therefore, my findings do not provide enough support to validate the 'island rule' for the assessed birds of the Australian, New Zealand and Antarctic region.

Keywords: island evolution, island biogeography, island ecology, insular morphological shift, meta-analyses, relative insular body size.

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Chapter 1

Introduction

1.1 Literature Review

1.1.1 Islands: perfect 'natural laboratories'

Islands are characterized as being isolated, small-sized and relatively young, with exceptionally variable and unique biotic and abiotic features compared to mainland areas (MacArthur & Wilson 1967; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009). These distinctive characters make island (insular) colonizers prone to a reduction in genetic diversity, new genetic arrangements and genotypic variation from founder effects and other bottlenecks, and more influenced by genetic drift (Cox & Moore 2005; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009; Lomolino et al. 2010). These changes in the genetic and phenotypic pool of insular populations in combination with novel but limited insular resources enable island habitats to become the sites of dramatic evolutionary and ecological processes that have caught the attention of ecologists, evolutionary biologists and biogeographers around the world for several decades (MacArthur & Wilson 1967; Grant 1968; Williamson 1981; Grant 1998, 2001; McNab 2002; Scott et al. 2003; Filin & Ziv 2004; Schlotfeldt & Kleindorfer 2006; Whittaker & Fernández-Palacios 2007; Losos & Ricklefs 2009; Luther & Greenberg 2011; Greenberg et al. 2012; Greenberg & Danner 2012).

Islands have been considered to be excellent 'natural laboratories' for research on how life-history affects the evolution of species features, like body size, sexual dimorphism, growth rate, and clutch size (MacArthur & Wilson 1967; Mayr 1967; Case 1978; Filin & Ziv 2004; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009). Insular territories are well defined and are relatively simple in make-up compared to close mainland communities, and this relative lack of complexity has allowed scientists to develop and test ecological and evolutionary theories on these habitats (Lomolino et al. 2010). These theories on insularity can also be extrapolated to 'island like' habitats within continental land masses, which are increasingly common due to habitat fragmentation (Whittaker & Fernández-Palacios 2007; Lomolino et al. 2010). One of the most recognizable, and much studied, theories in biology originated from studies on islands. MacArthur and Wilson (1967) proposed the 'Theory of Island Biogeography', which attempted to explain the number of species in an insular ecosystem by relating the equilibrium of the rate of colonization and immigration to extinction, and the size of the island. The implications of this theory for natural science was such that it took a long time before studies that criticized or contradicted its universality were published, and it was shown that only part of this theory is valid (relation between island area

and biodiversity) (Cox & Moore 2005). This theory inspired a new island approach in ecological biogeography and it is still very much used in conservation for optimizing conservation areas (Gillespie & Clague 2009; Lomolino et al. 2010).

Islands represent only 3% of Earth's land surface but they contribute prominently to our planet's biodiversity (Fisher 2004; Gillespie & Clague 2009). In a list of most biologically valuable ecoregions, Olson and Dinerstein (1998) indicated that 22 out of the 200 most important ecoregions for biodiversity conservation are associated with islands. In regards to vegetation, 19 of the 234 centres of plant diversity and endemism are located on islands (WWF & IUCN 1994), and one in three of the world's most endangered plants species are endemic to insular habitats (Whittaker & Fernández-Palacios 2007). Extinction rates on islands are thought to be faster than on mainland regions (Kirkwood & O'Connor 2010). More than 90% of the bird species that have become extinct since AD 1550 were endemic to islands (BirdLife International 2000; Sax et al. 2005; Steadman 2006). Moreover, BirdLife International (2000) indicated that seven of the fifty countries with the highest number of threatened bird species are islands, and 22 out of the 76 endemic bird areas of the world, that have been recognized as conservation priorities, are located on islands (Stattersfield et al. 1998). Therefore, a comprehensive understanding of the natural processes occurring on islands urges for the protection of these highly important and fragile 'hotspots' of biodiversity (Lasserre 2004; Rosabal 2004).

1.1.2 Unique life on islands

Islands are colonised by species using active mechanisms, such as 'sweepstake' dispersal, or by more passive mechanisms, such as when passively carried by other biotic or abiotic forces, which includes anthropogenic introductions (Cox & Moore 2005; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009; Lomolino et al. 2010; Martínková et al. 2013). The successful colonisation of a new species on islands will depend on the organisms' ability to survive a journey over long distances by air or water, restricting insular biodiversity to chance and their own dispersal capability (Cox & Moore 2005).

Once an island has been colonised, the two general ecological-evolutionary responses of species to these isolated habitats are ecological release and density compensation (Whittaker & Fernández-Palacios 2007). On one hand, ecological release consists in the enlargement of range, habitat and/or resources conventionally used by organisms after arriving in a community where some members are absent (Gillespie & Clague 2009). It involves the loss of some features that are not currently useful for the species in the new insular environment (e.g., flightlessness of birds) and improving other features towards a much more convenient form (e.g., birds with larger bills) (Cox & Moore 2005; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009; Lomolino et al. 2010).

Density compensation on islands regulates island species due to the lack of mainland species (Gillespie & Clague 2009). Density compensation allows niche expansions and higher abundances to match the total population densities of all insular species to the those on the mainland (Cox & Moore 2005; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009; Lomolino et al. 2010). Because of their isolation and dissimilarity to mainland environments, species on islands tends to reflect episodes of founder effect, drift and strong selection to adapt to new habitats, which may lead to speciation and diversification (Blondel 2000; Schluter 2001; Thomas et al. 2009). All these processes involved in colonisation and adaptation of new species on islands make insular life taxonomically unusual and highly endemic (MacArthur & Wilson 1967; Mayr 1967; Whittaker & Fernández-Palacios 2007). Insular habitats hold unique forms of mainland flora and wildlife, like sunflowers that become woody shrubs and trees like those of the *Scalesia* Genus, insects that have lost the ability to fly like the cricket *Triamescaptor aotea*, ground-foraging bats like New Zealand Lesser Short-tailed Bat *Mystacina tuberculata*, pygmy elephants such as the Borneo *Elephas maximus borneensis*, and giant shrews inhabiting Sumatra *Crocidura lepidura* (Grant 1998; Whittaker & Fernández-Palacios 2007; Lomolino et al. 2010).

Islands have lower species diversity and fewer resources, such as food, in comparison to same sized mainland areas; as well as fewer competitive, predatory and parasite species (Grant 1965; Whittaker & Fernández-Palacios 2007; Foufopoulos et al. 2011; Pérez-Rodríguez et al. 2013). These insular conditions cause distinctive phenotypes described by Adler and Levins (1994) as the 'island syndrome'. The island syndrome was first described for small rodents but then generalised to all vertebrates, and it involves a variation of morphological, physiological and behavioural types as well as life-history traits (Foster 1964; Grant 1968; Van Valen 1973a; Adler & Levins 1994; Blondel 2000; Clegg & Owens 2002). The evolution of greater ecological and morphological variation allows insular species to capture more resources than their mainland equivalents (Grant 1965; Van Valen 1965; Whittaker & Fernández-Palacios 2007; Losos & Ricklefs 2009).

1.1.3 The 'island rule' and other insular morphological shifts

In order to understand the effects that islands have on wildlife, many studies have focused on the morphological differences between insular species and their closest mainland counterparts (Blondel 2000; Grant 2001; Robinson-Wolrath & Owens 2003; Scott et al. 2003; Lomolino 2005; Losos & Ricklefs 2009; Lomolino et al. 2012). One of the most studied insular effects is the evolution of body size. Changes in this trait have a strong influence on other traits associated with immigration, ecological interactions, physiology and requirement of resources (Lomolino 1985; McNab 2002), thus body size and its variation are of great relevance to both ecological and evolutionary studies (Raia & Meiri 2011).

A well-known study on the variation in animal body size on islands by Foster (1964) described a pattern for rodents and small marsupials to become larger on islands in comparison to closely related mainland species, while carnivores, lagomorphs and artiodactyls tended to become smaller. Later, (Van Valen 1973b) named this tendency the 'island rule'. This rule states that insular vertebrates evolve towards an intermediate or 'optimal' body size relative to their mainland counterparts; therefore, large-bodied species tend to become smaller (i.e., dwarfism), while small bodied species tend to become larger (i.e., gigantism) relative to the mean size of their mainland counterparts (Heaney 1978; Lomolino 1985; Clegg & Owens 2002; Lomolino 2005; Boyer & Jetz 2010). A change in body size will allow species to optimize their energy usage towards reproduction, after satisfying their requirements for growing and maintenance (Boback & Guyer 2003; Lomolino 2005). These changes in body size represent a strategy to better exploit the limited insular resources with little to no pressure from interspecific competitors and predators (Grant 1965; Whittaker & Fernández-Palacios 2007).

Morphological trends on islands are the outcome of a combination of convergent factors across different spatial and temporal scales (Figure 1.1) (Lomolino 2005; Lomolino et al. 2012). Researchers have argued that insular morphological shifts dictated by the 'island rule' take place due to changes in feeding ecology, intraspecific and interspecific competition, energetic constraints and physiological optimisation (Selander 1966; Adler & Levins 1994; Dayan & Simberloff 1998; Blondel 2000; Clegg & Owens 2002; Lomolino et al. 2012; Lomolino et al. 2013). On one hand, a body size increment in small-bodied species has been related to intense intraspecific competition and high population densities characteristics from islands. On the other hand, a body size decline in large-bodied species has been considered to be an adaptation for heat loss and a method to reduce energy expenditure (Grant 1968; Case 1978; Clegg & Owens 2002; McNab 2002; Scott et al. 2003; Boyer & Jetz 2010; Symonds & Tattersall 2010; Wright & Steadman 2012; Greenberg & Danner 2013).

Additionally, trends towards dwarfism or gigantism by insular vertebrates have been directly related to the difference in resource availability between island and mainland (Case 1978; Myers et al. 2010; Raia et al. 2010b). The resource availability hypothesis indicates that the body size of an insular species depends directly on the amount of food available (Case 1978). Species are expected to reduce their size when resources are limited, and increase their size when they are bountiful. Moreover, vertebrates have a tendency to change their niche by becoming more generalist in the absence of interspecific competitors and predators (Soule & Stewart 1970; Heaney 1978; Dayan & Simberloff 1998; Grant 1998, 2001; Scott et al. 2003; Whittaker & Fernández-Palacios 2007; Raia et al. 2010b). The predator release hypothesis indicates that small colonist species lineages will tend to enlarge their size in the absence of predators (Lomolino 2005). An increment in body size would take

place because being small to hide from predators is no longer necessary for survival, as well as large body size being better placed to exploit insular resources (Figure 1.1).

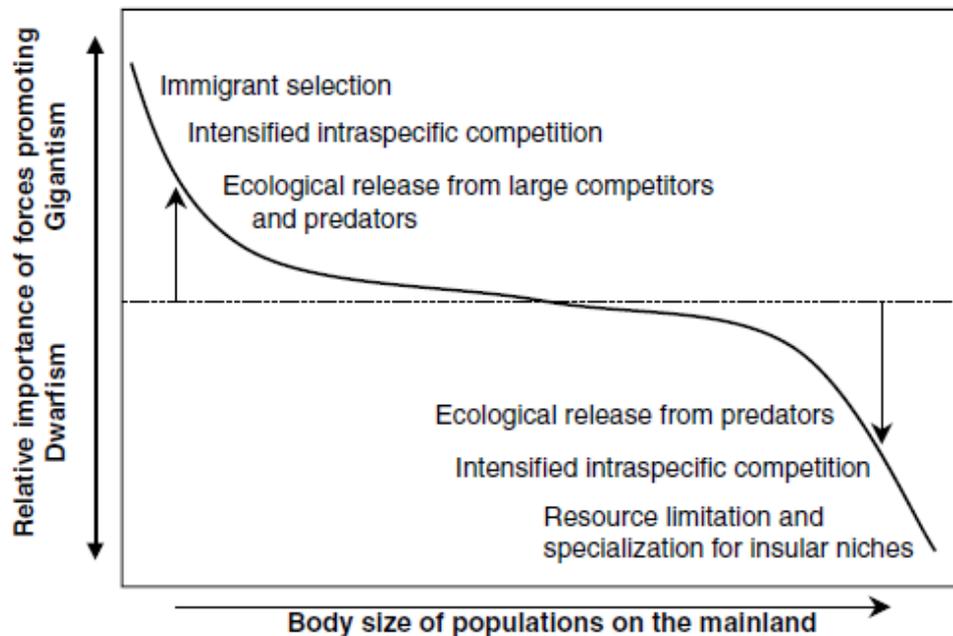


Figure 1.1 Factors influencing on the insular body size trends stated by the ‘island rule’ (from Lomolino (2005)).

Van Valen (1965) proposed the niche variation hypothesis which states that a population that varied morphologically or physiologically may coexist due to a wider niche in the absence of competitors. In contrast to mainland, islands are more variable in size and topography leading to more habitats and a greater range of niches (Grant 1971). Therefore, certain morphological traits are the result of adaptations to these new niches. For example, birds tend to develop larger bills and tarsi in order to expand their niche (Grant 1965; Van Valen 1965; Luther & Greenberg 2011). Moreover, genetic variation within a population allows for selection to occur as a response to stressful conditions, such as competition, predation or changes in the environment (Frankham 1997). In comparison to mainland populations, insular populations contain less genetic diversity due to several factors, such as bottlenecks in the population, genetic drift and isolation, and these factors are more pronounced in islands that are smaller or more isolated or when insular species have lower dispersal rates (Boessenkool et al. 2007).

Another insular morphological shift associated with the ‘island rule’ is the variation in the degree of sexual dimorphism (Roulin & Salamin 2010). Larger divergences between males and females of the same species on islands are a result of the lower genetic variation on insular habitats and a reduction in sexual selection, which increases the risk of extinction by favouring mating success

over survival (Griffith 2000; Morrow & Pitcher 2003). Greater degree of sexual dimorphism in insular species been considered to be a response to less interspecific competition for food and a strategy for occupying more morphological space than other species (Selander 1966; Dayan & Simberloff 1998; Butler et al. 2007; Cook et al. 2013).

Sexual dimorphism in body size or sexual size dimorphism (SSD) occurs to reduce intraspecific competition between males and females for limited food resources (Selander 1966; Schlotfeldt & Kleindorfer 2006; Butler et al. 2007). SSD is commonly associated with differential niche utilization between sexes which allows a population to persist in new environments by exploiting a higher diversity of nutrients (Schlotfeldt & Kleindorfer 2006). Because of limited resources, high population density and intensive intraspecific competition, SSD tends to become stronger on islands as a method to exploit vacant niches (Selander 1966; Dayan & Simberloff 1998; Butler et al. 2007). In birds, bills size variation between sexes is greater on islands than for similar mainland species as a strategy against high intraspecific competition by sequestering a wider range of available resources, and is thought to be influenced by the physical characteristics of each island, such as area and isolation (Soule & Stewart 1970; Willson et al. 1975; Cook et al. 2013; Greenberg & Danner 2013; Luther & Greenberg 2014).

1.1.4 Abiotic features influencing insular species evolution

Environmental and physical features of islands influence the ecology and evolution of insular species (Grant 1998; Cox & Moore 2005; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009; Lomolino et al. 2010). The 'Theory of Island Biogeography' recognized that the number of species on islands will increase with size but decline with isolation (MacArthur & Wilson 1967). Schoener (1976) qualified the species-area relationship as one of the few laws of community ecology. The relationship between species richness and island area is a much studied pattern where species number will rise with area, irrespective of the taxonomic group (Schoener 1976). According to MacArthur and Wilson (1967), a larger area will include new habitats with host specialized species restricted to those environments, therefore increasing the total number of species. The relationship between species and level of isolation is not as clear as the one between species-area. However, it has been recognized for many taxonomic groups and ecosystems that species richness has a strong negative relationship with isolation (i.e., more distant from mainland), mainly because of a decline in successful dispersal opportunities (MacArthur & Wilson 1967).

The size and remoteness of islands have also been associated with their resource availability, species richness and colonization probability (Lawlor 1982; Meiri 2007). Moreover, early studies found that these insular features play a very important role in the body size evolution of mammals, particularly for morphological changes (Heaney 1978; Lawlor 1982; Lomolino 1985). The 'island

syndrome' will be expressed more intensely on islands that are not large enough to resemble mainland regions, and on islands that are more distant from continental landmasses (Adler & Levins 1994). Nevertheless, Meiri et al. (2005a) found no consistent pattern of morphological variation for insular carnivores related to those two abiotic characteristics. Some studies have demonstrated significant variation in body size and reproductive traits, such as clutch size and time of parental care, in insular wildlife in comparison to mainland taxa, which have been correlated with each island's age, origin, area and isolation (Blondel 2000; Clegg & Owens 2002; Lomolino 2005; Covas 2012; Novosolov & Meiri 2013).

Area and distance from mainland have been criticized as being measurements of space and not of place, as the information they provide is only of size and location but not of the more complex characteristics inside each island and its surroundings (Cox & Moore 2005; Lomolino et al. 2010). Therefore, several studies have suggested the need to use variables that better reflect the ecological and biogeographic features of an island (MacArthur & Wilson 1967; Walter 2004; Diver 2008). Island climate is mostly determined by the sea surface temperature (SST) because the air temperatures on islands oscillate accordingly to variations in the temperature of adjacent waters (Gaston et al. 2005). SST has been used as an indirect measure of productivity and nutrients present on insular habitats (Carrillo et al. 1997), and is also found to have major influence in demography, reproduction, feeding ecology and life history traits of sea birds (Barbraud & Weimerskirch 2001; Sandvik et al. 2008) and sea turtles (Kershaw 2008b).

1.1.5 Testing the validity of the 'island rule'

In order to visualize 'island rule' patterns in vertebrates previously recognized by Foster (1964) and Van Valen (1973b), Lomolino (1985) expressed the degree of body size divergence as the relative insular body size (SR), which is equivalent to the 'percent divergence' used by Lawlor (1982). SR was calculated as the ratio between the mean body weight of an insular population (S_i) and the mean body weight from its closest mainland relative (S_m). By making simple comparison between SR and unity, 'gigantism' or 'dwarfism' was determined (i.e., $SR > 1$ or $SR < 1$, respectively). In order to test the statistical significance of body size patterns, Lomolino (1985) proposed the regression of the body size of insular species on the body size of their mainland counterparts:

$$\log S_i = k_0 + k_2(\log S_m),$$

where S_i and S_m are the insular and mainland mean body size, correspondingly, k_0 the intercept, and k_2 the slope of the regression. This log-log model was used in order to normalize the data. A slope k_2 significantly less than one will confirm the presence of morphological patterns stated by the 'island rule'. By performing these and other similar statistical analyses, scholars have supported the

'island rule' for mammals (Ashton et al. 2000; Lomolino 2005; Meiri et al. 2006; Bromham & Cardillo 2007), reptiles (Boback & Guyer 2003; Lomolino 2005), and birds (mainly Passerines) (Grant 1968, 1971; Clegg & Owens 2002; Meiri & Dayan 2003; Lomolino 2005). Nonetheless, Meiri et al. (2008) tested the validity of the 'island rule' for mammals, including a phylogenetic component, and found that insular body size variations were clade-specific patterns, diminishing the generality of the 'island rule'.

For many years the 'island rule' was not considered a general pattern for insular birds, but rather a trend found only in bill enlargement (Mayr 1963; Case 1978; Abbott 1980; Williamson 1981; Grant 1998; Blondel 2000; Whittaker & Fernández-Palacios 2007). However, more recent studies that include measurements of body weight as well as bill, wing, skull, teeth and tarsus length, mainly from Passeriformes species, have recognized that insular shifts in some of these traits follow the patterns dictated by the 'island rule' (Clegg & Owens 2002; Lomolino et al. 2012).

1.1.6 Meta-analyses in ecology

Meta-analysis is a remarkable tool in ecology that allows researchers to develop analyses of data with a higher statistic power and recognize trends at a larger scale than other statistical analyses which ignore sample size and only take into consideration statistical significant studies like vote counting; as well as to examine heterogeneity and make decisions based on quantitative evidence (Stewart 2010). Meta-analyses have been broadly used in medical research and social sciences since the 1970s, but only started to be applied in the ecology and conservation fields in the 1990s (Fernandez-Duque & Valeggia 1994). In comparison to traditional statistical tools used in the natural sciences, like vote counting, meta-analyses orientate more to the needs of a research when synthesizing the results of different studies and is data-based as it puts a weight to each considered study (Harrison 2011). Meta-analyses aim to develop an accumulated and more powerful null hypothesis test, estimate mean parameters, and assess the relation between species parameters and different environmental and biological factors (Osenberg et al. 1999). In a meta-analysis, effect sizes from each study, which are more informative variables (i.e. weighted based on their sample sizes) than the ones used on vote counting, are calculated, combined and compared. This allows meta-analysis to reduce the probability of making type II errors (i.e. failing to reject the null hypothesis when it is false) which can have more far-reaching consequences than type I errors (i.e. rejecting the null hypothesis when it is in fact true) in the conservation field as real effects may not be detected (Fernandez-Duque & Valeggia 1994; Harrison 2011).

Meta-analyses allow a quantitative synthesis to be made of data from different studies and to calculate a mean effect size of the explanatory variable. Meta-analyses also quantify how much variation in the response variable is caused by the experiments and explains this variation with

defined moderator variables (Côté & Sutherland 1997; Ferreira González et al. 2011; Harrison 2011). The obtained mean effect size in a meta-analysis is not a simple mean of the results of different studies but a weighted mean as this analysis takes into consideration the variability within and between the included studies (Ferreira González et al. 2011).

The models used in meta-analyses are fixed-, random-, or mixed-effects (Gurevitch & Hedges 1999). The main difference between the fixed- and random-effects models is that the former considers that inter-study variation of the effect sizes are fixed and caused only by sampling error; while the later assumes that the effects of evaluated studies variation on the effect sizes are random. A random-effects model is more appealing for ecological studies as the actual effects are expected to vary between different ecological systems (Gurevitch & Hedges 1999). Moreover, the mixed-effect models combine random variation among the evaluated studies within a category with fixed variation among categories (Gurevitch et al. 2001), and is, therefore, more convenient for evaluating within- study differences when the selected studies are not expected to be homogeneous.

1.2 Rationale

Even though the 'island rule' has been validated for many vertebrate groups, there has been debate about whether it applies to all avian orders. Most studies that test the 'island rule' on birds have focused on the order Passeriformes (Grant 1965; Robinson-Wolrath & Owens 2003; Scott et al. 2003; Lomolino 2005; Luther & Greenberg 2011). What is more, significant differences between body size of insular and mainland related vertebrate species were found by comparing a variety of morphological measurements, but in non-passerines significant differences have only been found using body weight and bill length (Clegg & Owens 2002; Meiri et al. 2006). Therefore, a critical examination of the 'island rule' and its validity the various avian Orders has been recommended (Lomolino 2005; Meiri et al. 2006; Gillespie & Clague 2009; Lomolino et al. 2010).

Greenberg and Danner (2013) recognized that bill size dissimilarities between sexes had different degrees of variation among different islands but not within mainland regions. They proposed that bill size variation was related to island size and maximum temperature. Studies to date that have evaluated sexual size dimorphism on bill length have only done so for species within the order Passeriformes (Cook et al. 2013; Greenberg & Danner 2013; Luther & Greenberg 2014). An evaluation of sexual size dimorphism variation of bill size, and other traits, for bird species from other Orders and regions is needed.

In regards to the abiotic variables used to explain the insular morphological shifts dictated by the 'island rule', island area and isolation from a mainland have been shown to have a key role in the evolution of body size of insular species (Heaney 1978; Lomolino 1985; Adler & Levins 1994; Clegg &

Owens 2002; Lomolino 2005). However, the use of mere measurements of island size and distance from the mainland has been criticized for their lack of ecological and biogeographic significance (MacArthur & Wilson 1967; Walter 2004; Cox & Moore 2005; Diver 2008; Lomolino et al. 2010). Sea surface temperature is an abiotic feature that has been used as a predictor of islands climate and productivity (Carrillo et al. 1997; Gaston et al. 2005). Therefore, I will also evaluate the influence of the sea surface temperature (SST) in the body size evolution of insular birds.

1.3 Statement of Research Interest

In order to test the validity of the 'island rule' for many avian Orders from the Australian, New Zealand and Antarctic (ANZA) region, I used data from previous studies to compare morphological measurements from island and mainland bird species registered for the area.

1.4 Research Aim

I aim to identify and explain trends in the morphological variation of insular birds from the Australian, New Zealand and Antarctic region in order to test the validity of the 'island rule'. I will analyse morphological measurements from islands and mainland avifauna within the region. The variation between sexual dimorphism of island and continental lineage pairs of bird species will be evaluated. Additionally, the relationship between avian morphological measurements and abiotic characteristics of each island will be assessed.

1.5 Research Objectives

- Assess the significance and trends of the variation between morphological structures, such as body weight, bill length, tarsus length, and wing length, of closely related bird species from mainland and island areas in the Australian, New Zealand and Antarctic region.
- Determine if the degree of avian sexual size dimorphism differs between mainland and island areas in the Australian, New Zealand and Antarctic region.
- Determine if insular abiotic characteristics, such as size, sea surface temperature and distance from mainland, influence variation between morphological structures of closely related bird species from mainland and island areas in the Australian, New Zealand and Antarctic region.

1.6 Hypotheses

- Significant differences between morphological measurements of related bird species from island and mainland are expected.

- Consistent trends for large-bodied birds towards dwarfism and small-bodied birds towards gigantism that prevail at the family and order level are predicted, validating the 'island rule' patterns for the avifauna of the ANZA region.
- Greater bill size variation between male and female insular birds compared to mainland counterparts is anticipated for the avifauna of the ANZA region, as in other regions. Greater insular sexual size dimorphism for the other traits will presumably be found too.
- Significant relationships between insular body size variations and abiotic insular features, such as island area, distance from mainland and sea surface temperature, are anticipated as found in previous studies.

Chapter 2

Methods

2.1 Area of study

I evaluated birds from the Australian, New Zealand and Antarctic (ANZA) region. This region was delimited by the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) editors based on the bird species' distribution and on the quantity and quality of the contribution of each area to the described species for the region (Marchant & Higgins 1990). The ANZA region covers Australia (continental shelf) and its adjacent islands, New Zealand and its islands from the Kermadec Group to Campbell Island, the Antarctic Continent, and the sub-Antarctic islands, Cocos-Keeling, Christmas, Lord Howe, Norfolk Islands, and reefs of the Coral Sea (Figure 2.1) (Marchant & Higgins 1990). After filtering my data as described in the next section, I had information from 40 islands within this region (Figure 2.2).

Most of the islands within the ANZA region were given World Heritage status during the 1990s due to their high endemism of bird species and their critical biological processes, such as biological adaptation and evolution (United Nations Educational Scientific and Cultural Organization 1999; Gillespie & Clague 2009). Almost 30% of these islands remain free from humans and predators, and are considered a sanctuary for many avian species (Clout 2001; Boessenkool et al. 2007). Successful non-native predator eradication programs have taken place in some of these insular habitats where introduced species were driving native fauna, specially birds, into extinction (Bellingham et al. 2010; Buxton et al. 2014). Islands in this region are also recognized for their importance as breeding colonies for many endangered seabird species, like petrels, albatross and penguins, as well as vital resting areas for migratory birds (Gillespie & Clague 2009; Kirkwood & O'Connor 2010). However, island habitats are suffering the highest rates of extinction, especially of avifauna. According to a list of 23 extinct species from 2010, at least 19 were endemic to islands in this region (Kirkwood & O'Connor 2010). Subsequently, an evaluation of the evolutionary and ecological processes occurring in these islands will provide information that could contribute towards the conservation and management of bird species from the ANZA region.

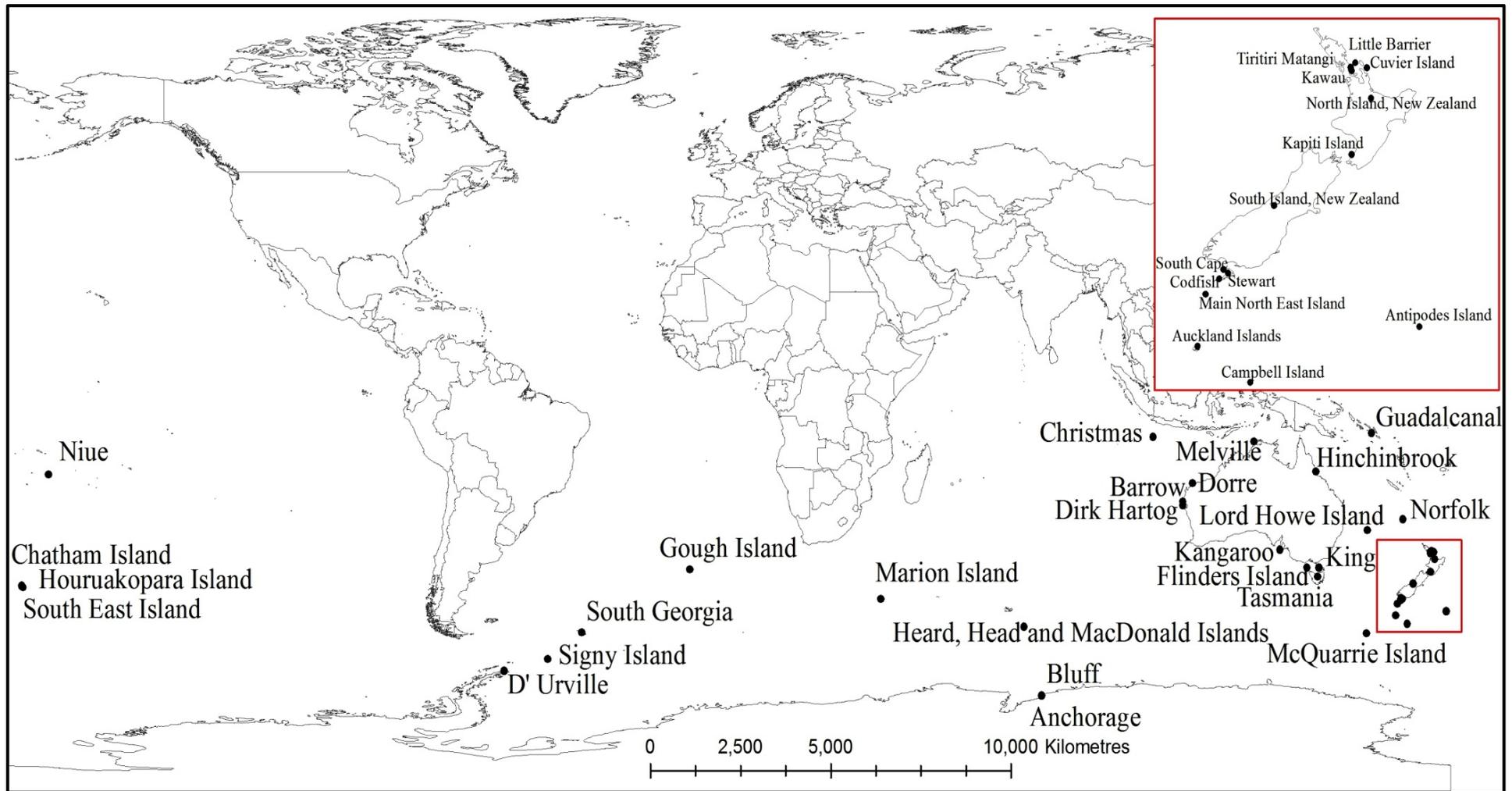


Figure 2.2 Map of the studied islands within the ANZA region.

2.2 Data collection

The information used for my analyses was taken from previous published information. The collected data consisted of taxonomic and morphological information of closely-related bird species from mainland and islands within the ANZA region, as well as physical and environmental information from islands. After the filters described in this section, the final data consisted of 242 mainland/island bird species pairs for wings length from 37 islands, 125 pairs for bill length from 29 islands, 190 pairs for tarsus length from 32 islands, and 146 pairs for weight measurements from 28 islands. The data was compiled in Microsoft Excel V.2010 (see Table 2.1 for an example of data entry and Supplementary Material for full datasets).

2.2.1 Bird data

The selected bird morphological measurements to be evaluated in this study were body weight (in grams), bill length (in millimetres), tarsus length (in millimetres), and wing length (in millimetres) of adult birds. These measurements have previously been used in the evaluation of the 'island rule' for birds in other studies as they are good indicators of body size, and their evolution on islands was affected by insular biotic and abiotic characteristics (Grant 1968, 1971; Clegg & Owens 2002; Meiri & Dayan 2003; Lomolino 2005). These measurements are also indicators of changes on feeding habits like prey size and perch foraging, and loss of flight ability (Grant 1968, 1971). Moreover, taxonomic information for each bird species (i.e., order and family) was also integrated to analyse patterns of morphological variation in relation to their taxonomic groups, similar to what Meiri et al. (2008) did to analyse similar questions in mammals. Mainland/island taxon pairs were either from the same species or their most closely related sister-taxa, following the classification of Christidis and Boles (2008).

Only data taken from sexed adults was collected (Meiri et al. 2008) in order to reduce bias and noise. A preliminary analysis showed that data from some unsexed species did not contribute significantly to my results. Similarly, only data from extant species was included as fossils cannot usually be accurately sexed (Raia & Meiri 2006) and only a few body size estimates for extinct Pacific islands birds have been published (Boyer & Jetz 2010). Also, because the aim of this research was to analyse the two morphological patterns stated by the 'island rule' (i.e. large animals becoming smaller and small animals becoming larger on islands), the data was further divided into small and large animals. Clegg and Owens (2002) also separated their data according to the mean size of their database, while Meiri et al. (2008) used the median as reference for their data division. I did a more objective data split by comparing the mean body length of each mainland species to the mean body length of their respective Family (see Appendix A). This data partition should recognize patterns within each size range where past studies have only found evidence for the enlargement of small

species (Cassey & Blackburn 2004). Finally, the author of each description for insular and mainland species was included for further use in the meta-analyses.

Source of Information

The bird data described in the previous section were obtained from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB), volumes one to seven (Marchant & Higgins 1990; Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Higgins et al. 2001; Higgins & Peter 2002; Higgins et al. 2006). The HANZAB collection was published between 1990 and 2006 by Oxford University Press for the Royal Australasian Ornithologists Union (RAOU), Australia's oldest conservation organisation.

According to Del Hoyo et al. (2007a), the HANZAB took 20 years of work and provides relevant information on avifauna of the ANZA area from a broad variety of sources including theses, unpublished data and personal observations. It gathers biological information based on data published for the region's 957 species (almost 10% of the world's avifauna), including recently extinct species, recorded for Australia, New Zealand, Antarctic and all their offshore islands; the sub-Antarctic islands; and an assortment of other associated islands (Marchant & Higgins 1990). The HANZAB includes material regarding bird's habitat, distribution and population, food, social and behaviour, measurements and others. More specifically, the handbook measurements and weights sections contain a systematic summary of the data for each species. Mean, minimum and maximum size, standard deviation, sample size and the location where they were taken are given for each morphological measurement (Fig. 2.3). I used sex and location data to identify each species as well as the mean, standard deviation and sample size data as these are the measurements required for subsequent analyses. Thus, the HANZAB is the most accessible and accurate source of information for obtaining most of the data required for the proposed study.

Body length data was used to determine if species were small or large was obtained from the Handbook of Birds of the World, volumes 1 to 16 (Del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, 2002; Del Hoyo et al. 2003, 2004, 2005, 2006, 2007b, 2008, 2009, 2010, 2011). This book contains an introductory, detailed text for all bird families, which included the mean body length for each of these groups. Even though the HANZAB also included a mean body length for most of the described Families, sometimes this mean had been calculated from only the species present of the ANZA region, therefore the Handbook of Birds of the World was the best available source for these measurements.

Table 2.1 Example of data entry. This record shows bill measurements for *male Coturnix ypsilophora australis* and its Tasmanian counterpart *Coturnix ypsilophora ypsilophora*.

Order	Family	mainland spp.	sex	size	mainland region	author 1	mainland mean (mm)	mainland std dev	mainland sample size
GALLIFORMES	PHASIANIDAE	<i>Coturnix ypsilophora australis</i>	M	S	se Australia	Marchant & Higgins, 1993	13.2	0.75	15

insular spp.	island name	author 2	insular mean (mm)	insular std dev	insular sample size	lat	long	island area (sq. km.)	distance mainland (km)	sea T (°C)
<i>Coturnix ypsilophora ypsilophora</i>	Tasmania	Marchant & Higgins, 1993	13.9	1.05	18	-42.00	146.75	68401.00	200.00	26.27

MOULTS Based on c. 130 skins (ANWC, AWMM, HLW, MV, NMNZ, QVM, TMAG). Sequences of moults and plumages similar to Stubble Quail, though occurrence of pre-breeding (pre-alternate) moults unconfirmed; however, at least two skins in body-moult when primaries not active. **Adult post-breeding** (Definitive pre-basic). Complete or nearly so. Primaries, outwards; one or two active at once. Outer 1–3 primaries often retained, and then moult apparently arrested, resuming from p1 next pre-basic. Eight skins showed evidence of two simultaneous waves in primaries. Secondaries, inwards; centres, unknown. Timing varies greatly; generally later and more varying farther N and probably depends on local conditions; peak of primary-moult, Jan.–Apr. in Tas. and NZ; Feb.–July in se. Aust.; Feb.–Oct. in n. and ne. Aust. **Post-natal** Complete. Timing depends on date of hatching. Primaries, simultaneous; inners ahead of outers; pins appear soon after hatching; rate of moult has not been studied in detail but probably similar to Stubble Quail. Fly at c. 10 days (Seth-Smith 1905); first body-feathers on breast and rump; feathers of head, last (S.J.S. Debus). **Post-juvenile** (First pre-basic). Partial; outer three, sometimes four, rarely five, juvenile primaries and usually all juvenile greater primary coverts, retained; rarely some inner primary coverts replaced. Primaries, outwards. Timing depends on date of hatching. Begins before post-natal moult complete while juvenile p9 and p10 still growing.

MEASUREMENTS Skins (ANWC, AWMM, HLW, MV, NMNZ, QVM, TMAG). Sexing based on labels and plumage of upperparts; birds included only if both criteria agree. All samples combine adults and first immatures. Tail, approximate.

Subspecies *australis*: (1) se. Aust. (Vic., NSW, se. Qld), N to c. 25°S; (2) ne. Qld, N of c. 20°S; (3) n. and nw. Aust., N of c. 20°S; (4) sw. WA.

	MALES	FEMALES	
WING	(1) 98.3 (3.00; 93–105; 16) (2) 93.0 (3.12; 89–97; 8) (3) 93.0 (3.70; 88–98; 9) (4) 91, 102	100.3 (4.83; 91–106; 17) 95.4 (2.12; 40–45; 7) 93.6 (3.04; 87–97; 13) 101, 103, 103	ns ns ns
8TH P	(1) 68.2 (2.48; 64–74; 13) (3) 65.0 (4.47; 59–70; 5)	68.3 (3.65; 62–74; 15) 62.8 (3.04; 59–67; 6)	ns ns
TAIL	(1) 42.1 (4.79; 36–52; 14) (2) 39.7 (3.42; 59–70; 5) (3) 38.0 (3.42; 34–45; 8)	43.0 (3.98; 34–48; 15) 42.1 (2.12; 40–45; 7) 38.7 (2.41; 34–43; 11)	ns ns ns
BILL F	(1) 13.2 (0.75; 12.0–14.2; 15) (2) 13.0 (0.59; 12.0–13.7; 8) (3) 13.0 (0.68; 12.0–14.4; 9) (4) 13.0, 13.0	13.2 (0.46; 12.4–14.2; 17) 13.0 (0.76; 11.5–13.8; 7) 13.2 (0.57; 12.0–14.0; 13) 12.6, 13.1, 14.0	ns ns ns ns
TARSUS	(1) 22.6 (1.22; 19.9–23.9; 16) (2) 22.1 (0.66; 21.0–22.6; 7) (3) 22.1 (1.14; 19.6–23.4; 9) (4) 20.2, 22.2	22.6 (0.88; 21.2–24.0; 15) 22.4 (0.87; 21.0–32.7; 7) 21.2 (1.00; 19.6–22.5; 13) 22.7, 22.9, 24.7	ns ns ns ns
TOE	(1) 20.5 (1.21; 19.0–23.6; 14) (2) 19.9 (1.17; 18.9–21.9; 6) (3) 19.3 (0.89; 17.9–20.5; 9) (4) 19.1, 20.0	20.5 (0.67; 19.2–21.6; 13) 20.5 (1.28; 18.1–21.3; 6) 19.3 (1.02; 17.5–21.0; 13) 19.9, 20.4	ns ns ns ns

Nominate *ypsilophora*: (5) Tas.

	MALES	FEMALES	
WING	(5) 106.1 (3.04; 103–112; 15)	107.0 (4.06; 102–115; 9)	ns
8TH P	(5) 71.5 (2.38; 68–76; 14)	71.3 (2.71; 67–75; 10)	ns
TAIL	(5) 45.5 (2.88; 42–51; 17)	47.0 (2.16; 44–49; 4)	ns
BILL F	(5) 13.9 (1.05; 11.7–15.6; 18)	14.5 (0.74; 13.4–16.2; 10)	ns
TARSUS	(5) 23.6 (1.18; 21.3–26; 18)	25.0 (0.82; 23.5–26.3; 10)	*
TOE	(5) 21.5 (0.97; 19.5–23.0; 18)	21.5 (1.01; 20.0–23.4; 10)	ns

Subspecies undetermined: (6) NZ.

	MALES	FEMALES	
WING	(6) 99.4 (3.73; 89–105; 25)	92.6 (3.54; 93–104; 16)	ns
8TH P	(6) 66.4 (3.26; 57–72; 16)	66.8 (2.28; 63–69; 9)	ns
TAIL	(6) 44.3 (2.41; 40–50; 22)	43.5 (3.48; 37–50; 15)	ns
BILL F	(6) 12.9 (0.63; 11.2–13.9; 26)	12.8 (0.66; 11.4–13.5; 16)	ns
TARSUS	(6) 22.5 (1.43; 19.5–24.8; 25)	23.2 (1.13; 21.6–25.2; 17)	ns
TOE	(6) 20.0 (0.92; 18.5–21.9; 21)	20.2 (1.01; 18.5–21.8; 13)	ns

Literature contradictory on sexual dimorphism in size; these samples, though small, indicate little difference. Significant differences ($P < 0.05$) in: length of wing for males, and length of wing, bill and tarsus for females, between se. Aust. (*australis*) and Tas. (*ypsilophora*); length of wing for males between se. Aust. and ne. Qld; length of wing for males, and all but length of bill for females between se. Aust. and n. and nw. Aust.; length of wing, tail, tarsus and toe for males, and length of bill and toe for females between ne. Qld and Tas. and n. and nw. Aust. and Tas.; and all measurements, except tail-length, between NZ and Tas.; all other differences not significant. See Geographical Variation for discussion.

WEIGHTS All samples combine adults and first immatures; sexing based on labels and plumage of upperparts; birds included only if both criteria agree (from museum labels: ANWC, AWMM, HLW, MV, NMNZ, QVM, TMAG). For details of samples and sexing see Measurements.

Subspecies *australis*: (1) se. Aust. (Vic., NSW, se. Qld), N to c. 25°S; (2) ne. Qld, N of c. 20°S; (3) n. and nw. Aust., N of c. 20°S; (4) sw. WA.

	MALES	FEMALES	
(1)	98 (11.8; 80–123; 13)	103 (15.4; 85–140; 12)	ns
(2)	82 (5.7; 75–89; 4)	92, 96	
(3)	86 (2.39; 83–88; 5)	86 (10.5; 69–97; 6)	ns

Nominate *ypsilophora*: (5) Tas.

	MALES	FEMALES	
(5)	119 (14.1; 103–140; 7)	112 (10.6; 95–125; 9)	ns

Subspecies undetermined: (6) NZ.

	MALES	FEMALES	
(6)	104 (5.4; 95–108; 5)	95, 105, 117	

Significant differences: males, between se. Aust. and Tas. and between se. Aust. and n. and nw. Aust.; males, between ne. Qld and Tas; males and females, between n. and nw. Aust. and Tas.

STRUCTURE Large plump quail; in Tas., slightly larger than Stubble Quail; in s. mainland, similar in size to Stubble Quail; in N, smaller than Stubble Quail. Wing, short, broad; broader and with blunter tip than Stubble Quail. Marked step in trailing-edge between long outer primaries and shorter inner ones, which, with

Figure 2.3 Example of measurements and weight section of the HANZAB for *Coturnix ypsilophora australis* and its Tasmanian counterpart *C. y. ypsilophora* (From Marchant and Higgins (1993), p. 412).

2.2.2 Island data

In order to accomplish the third objective regarding testing abiotic moderators of insular morphological shifts, physical and environmental information of identified oceanic islands were incorporated into the database. This information consisted of island area (in square kilometres), distance from the nearest mainland (in kilometres), and sea surface temperature (in celsius). The first two variables have been tested as predictors of body size evolution of insular mammals (Heaney 1978; Lomolino 1985). As the sea surface temperature (SST) was obtained using the latitude and longitude from each island, this abiotic feature was used as a spatial variable that reflected also the climate and productivity of each island and its surroundings, overcoming the limitations of using only distance from mainland and island size data (MacArthur & Wilson 1967; Walter 2004; Cox & Moore 2005; Diver 2008; Lomolino et al. 2010). Moreover, SST has been previously used as an indirect predictor of body size evolution of insular reptiles (Carrillo et al. 1997).

As previous studies have indicated that the 'island rule' manifests to a greater degree on small islands (Lomolino 2005), a minimum island area was not considered. In contrast, big islands tend to have an effect on body size evolution very similar to mainland (Meiri et al. 2004; Badano et al. 2005; Lomolino 2005). Subsequently, recent studies have established a maximum island area of 50,000 sq. km. in order to evaluate the 'island rule' (Meiri et al. 2006; Meiri 2007). Nevertheless, for this study, the North and South Islands of New Zealand and Tasmania in Australia, whose areas are over 50,000 sq. km. but are at least 10 times smaller than Australia, were also considered to be islands when the mainland species source was Australia (Meiri 2007). Spatially close populations have shown dramatic differences in body size (Jessop et al. 2006), therefore, data from archipelagos were not included in the analyses. Only data that were recorded with certainty from individual islands were assessed, a similar approach to Meiri et al. (2008).

Source of Information

The island data described in the previous section was mainly obtained from the Island Directory of the World (United Nations Environmental Program 2010). This Directory was first developed in 1987-89, and contains information of almost 2000 of the significant oceanic islands of the world and more than 150 of those are within the ANZA region. The figures found in this Directory include those related to geographic location and climate needed for this study. The Bird Life International Data Zone (BirdLife International n.d.) and other sources were used to complement the required abiotic insular information for this research. Similarly, the sea surface temperature (SST) was obtained from the mean annual global sea surface temperature 2003 to 2007 dataset (Kershaw 2008a) using the latitude and longitude data from each island. This dataset is based on remotely-sensed images from the National Aeronautics and Space Administration's Ocean Colour database.

2.3 Data analyses

The statistical analyses of the obtained data was conducted using R V. 3.0.2 (R Core Team 2013). Because each trait was analysed independently, their values were used as such and not cubed like in past studies, when linear measurements were directly compared with the tri-dimensional mass measurement (Lomolino 1985; Meiri et al. 2008). All measurements were natural log- transformed before each analysis to normalise the data and stabilise the variance (see Supplementary Material for the R code used).

2.3.1 Objective 1: Assessing insular morphological shifts on birds

In order to identify significant differences in the morphological structures of closely related bird species from insular and mainland environments, as stated in the first Objective, I compared the mean of each morphological measurement for each pair of bird species with a paired *t*-test for each trait for all the bird species combined as well as for both small and large birds separately. In order to recognize patterns within clades, I repeated this test at the order and family level when there were more than 10 pairs in each group.

To test the occurrence of 'island rule' morphological patterns, the relative insular body size (SR) was calculated as the ratio of island body size (S_i) to mainland body size (S_m) (i.e., $SR = S_i/S_m$, as in Lomolino (1985)). SR values greater or smaller than 1 indicate an increase or reduction of insular species body size. Next, a regression model was tested for the $\log S_i$ and $\log S_m$ for each trait, using the 'offset' code in R to compare the regression slope against unity (i.e., a slope equal to 1). A slope significantly less than unity will confirm the morphological patterns stated by the 'island rule' (Lomolino 1985). I then plotted the regression of the relative insular size as a percentage of the mainland size against the mainland size in order to visualize graded dwarfism or gigantism trends as in Lomolino (1985).

2.3.2 Objective 2: Comparing the degree of sexual size dimorphisms between insular and mainland birds

In order to determine if sexual dimorphism is stronger or weaker on insular and mainland birds as indicated in the second objective, I calculated the sexual size dimorphism ratio for mainland and insular species (SSD_m and SSD_i, respectively) as the male-to-female ratio for each of the four traits as in Webster (1992). Therefore, only species with data for both male and female mainland and insular pairs were included in this analysis. A paired *t*-test was performed between the SSD ratio for each trait and each insular-mainland pair, for the combined and divided data. In order to recognize patterns within clades, I repeated this test at the order and family level when there were more than

five pairs in each group. Since SSD ratio is expected to be greater on islands, I used 'less' as the alternative hypothesis.

2.3.3 Objective 3: Testing the effect of moderators on avian insular morphological shifts

I performed meta-analyses using the Metafor package in R (Viechtbauer 2010) to complement the *t*-test performed for Objective 1. The meta-analysis allowed me to compare the data collected from many studies by calculating an effect size that reflects the weight of each study, as well as an overall effect size and its heterogeneity. The meta-regression allowed me to reduce this heterogeneity by including some explanatory variables (Côté & Sutherland 1997; Ferreira González et al. 2011; Harrison 2011). Therefore, the meta-analyses allowed me to analyse the morphological patterns of insular birds more deeply.

As an estimate of effect size I used the ratio of means (RoM), which Friedrich et al. (2011) described as is the ratio between the mean of the experiment and the mean of the control ($RoM = M_{exp}/M_{contr}$). The RoM method provides similar treatment effects and heterogeneity compared with the mean of differences and the standardised mean of difference methods, but less heterogeneity (Friedrich et al. 2011). For this study, I calculated RoM as the relative insular body size, which is the ratio between the insular mean and the mainland mean (i.e., $RoM = M_i/M_m$) for each trait in the combined data and both size groups separately, to evaluate the effect of insularity on bird evolution.

For the meta-analyses of my data, I assumed that each mainland-insular pair of closely-related species was an independent study whose authors were the combination of the mainland and insular data authors. To account for the lack of independence generated by phylogeny and species pairs (e.g., some mainland-island pairs were present more than once as there were data for both male and female), I ran meta-analytic models using the 'rma.mv' function. This multivariate modelling function allowed me to fit mixed-effects models by including the argument 'random = ~ 1|family/species_pair'. However, for the weight measurements of the combined and large species data I did not have adequate number of replications across the random effects so I tested meta-analytic models using the 'rma' function. Both of these models have a default restricted maximum likelihood (REML) estimator.

I first used a random-effects model, which assumes that the true effect size is different between studies and that the studies included in the meta-analysis represent a random sample of the effect sizes (Borenstein et al. 2009). The random-effects model allowed me to evaluate trends and relationships among the variables that could have not been recognized by the previous statistical

analyses. Using the natural base exponential of the resulting mean effect size, I obtained the mean relative insular body size (SR) for each trait, which allowed me to determine if the studied species were following the body size trends dictated by the 'island rule' (i.e., $SR > 1$ expresses insular gigantism and $SR < 1$ expresses insular dwarfism).

To test the effect of moderators on the obtained effect size I performed a meta-regression using the mixed-effect model. The meta-regression allowed me to evaluate the influence of insular abiotic characteristics, such as area, distance from mainland and sea surface temperature, on the morphological differences between island and mainland birds, as established in the third objective. Because the variables to be evaluated were in different units, a previous standardization using the 'decostand' function was performed. I also fitted a 'null', 'intercept only' model to compare the models with explanatory variables against it.

Finally, I used the small sample size corrected version of Akaike's information criterion (AICc) values obtained from the 'rma.mv' and 'rma' functions to compare and rank different competing models using area, distance from mainland and sea surface temperature as explanatory effects. The best models for each trait were selected based on the lowest AICc value. Moreover, the best model's worth was evaluated based on how different it was from the null model or the other models (e.g., at least more than 2 AICc points of difference) (Anderson 2008; Symonds & Moussalli 2011).

Chapter 3

Results

3.1 Objective 1: Assessing insular morphological shifts on birds

3.1.1 Species level

There were differences between island and mainland closely-related bird species for the four evaluated traits. For the analyses of all species combined, I obtained significant differences between mainland and insular species for wing, bill and tarsus length but not for weight measurements (Table 3.1). For the four traits, the majority of species had relative insular body size values greater than 1 (i.e., $SR > 1$), showing a predominant trend towards insular enlargement (Table 3.1). However, when testing for statistical validation of the 'island rule' patterns by regressing the insular size on mainland size (Lomolino 1985), the resulting slopes were significantly less than 1 only for bill and tarsus length (Table 3.1). Still, these slopes were very small, indicating only little variation between insular and mainland traits. Subsequently, my findings partially support my first and second hypotheses as the existing differences between morphological measurements of insular and mainland birds were not always significant and the trends towards dwarfism or gigantism were not consistent.

When the data were split based on their body length, mainland and insular body size differences between insular and mainland body sizes were only statistically significant in the *t*-test for bill and tarsus length of small birds (Table 3.2), and for wing length of large birds (Table 3.3). The number of insular species whose size remained the same as their mainland counterparts (i.e., $SR = 1$) was very low for the four traits in both small and large bird species, indicating a predominant trend towards insular size variation. There was a tendency for an insular body size increase showed by a majority of relative insular body size values greater than 1 (i.e., $SR > 1$) in small species for bill, tarsus and weight measurements, as well as in large species for wing and weight measurements. Conversely, there was a trend towards an insular body size reduction (i.e., $SR < 1$) for wing length in small species and bill for large species. In the case of tarsus for large species, the number of species with $SR > 1$ and $SR < 1$ was the same, demonstrating no insular body size variation (Table 3.3). The 'island rule' patterns were only statistically corroborated with the slope of the regression of insular size on mainland size significantly less than 1 (Lomolino 1985) for tarsus length in small species and for bill length in large species. However, the obtained slopes had very low values, demonstrating only slight size variation between insular and mainland traits.

Table 3.1 Outcome of *t*-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and Regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at the species level for all species combined.

Trait	n	<i>t</i> -test		N. of species with SR>1	N. of species with SR<1	N. of species with SR=1	Regression Si against Sm (testing slope against 1)	
		t value	p value				slope	p value
Wing	242	-2.040	0.0424	126	114	2	-0.001	0.850
Bill	125	-2.363	0.0197	66	56	3	-0.059	0.001
Tarsus	190	-2.333	0.0207	107	77	6	-0.037	0.002
Weight	146	-0.481	0.6290	81	61	4	-0.015	0.360

Table 3.2 Outcome of *t*-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at the species level for small species.

Trait	n	<i>t</i> -test		N. of species with SR>1	N. of species with SR<1	N. of species with SR=1	Regression Si against Sm (testing slope against 1)	
		t value	p value				Slope	p value
Wing	172	-1.217	0.226	84	86	2	-0.0036	0.729
Bill	89	-2.925	0.004	53	34	2	-0.0518	0.071
Tarsus	121	-2.189	0.031	74	44	3	-0.0419	0.019
Weight	104	-1.015	0.313	52	48	4	-0.0091	0.465

Table 3.3 Outcome of *t*-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at the species level for large species.

Trait	n	<i>t</i> -test		N. of species with SR>1	N. of species with SR<1	N. of species with SR=1	Regression Si against Sm (testing slope against 1)	
		t value	p value				Slope	p value
Wing	70	-2.469	0.016	42	28	0	0.001	0.898
Bill	36	1.277	0.210	13	22	1	-0.049	0.000
Tarsus	69	-0.921	0.361	33	33	3	-0.034	0.053
Weight	42	0.108	0.914	29	13	0	-0.028	0.556

Figure 3.1 illustrates visually the results of the regressions of the insular measurements as percentage of the mainland measurements against the mainland measurements for all species combined. The morphological shifts associated with the 'island rule' were identified for bill and tarsus length. For bill and tarsus length of small species, the resulting SR percentages were greater than 100%, indicating a trend towards gigantism. Conversely, but not as clear as for the small species, large species had bill and tarsus lengths with SR percentages lower than 100%, indicating a trend towards dwarfism.

For the divided data, the morphological shifts associated with the 'island rule' can only be recognized for tarsus and bill length in both small and large species (Figures 3.2 and 3.3, respectively). For small values of mainland tarsus and bill lengths, the corresponding insular values were above the 100% line, indicating an insular enlargement (Figure 3.2). For large values of mainland tarsus and bill lengths, the corresponding insular values were below the 100% line, indicating an insular shrinkage (Figure 3.3).

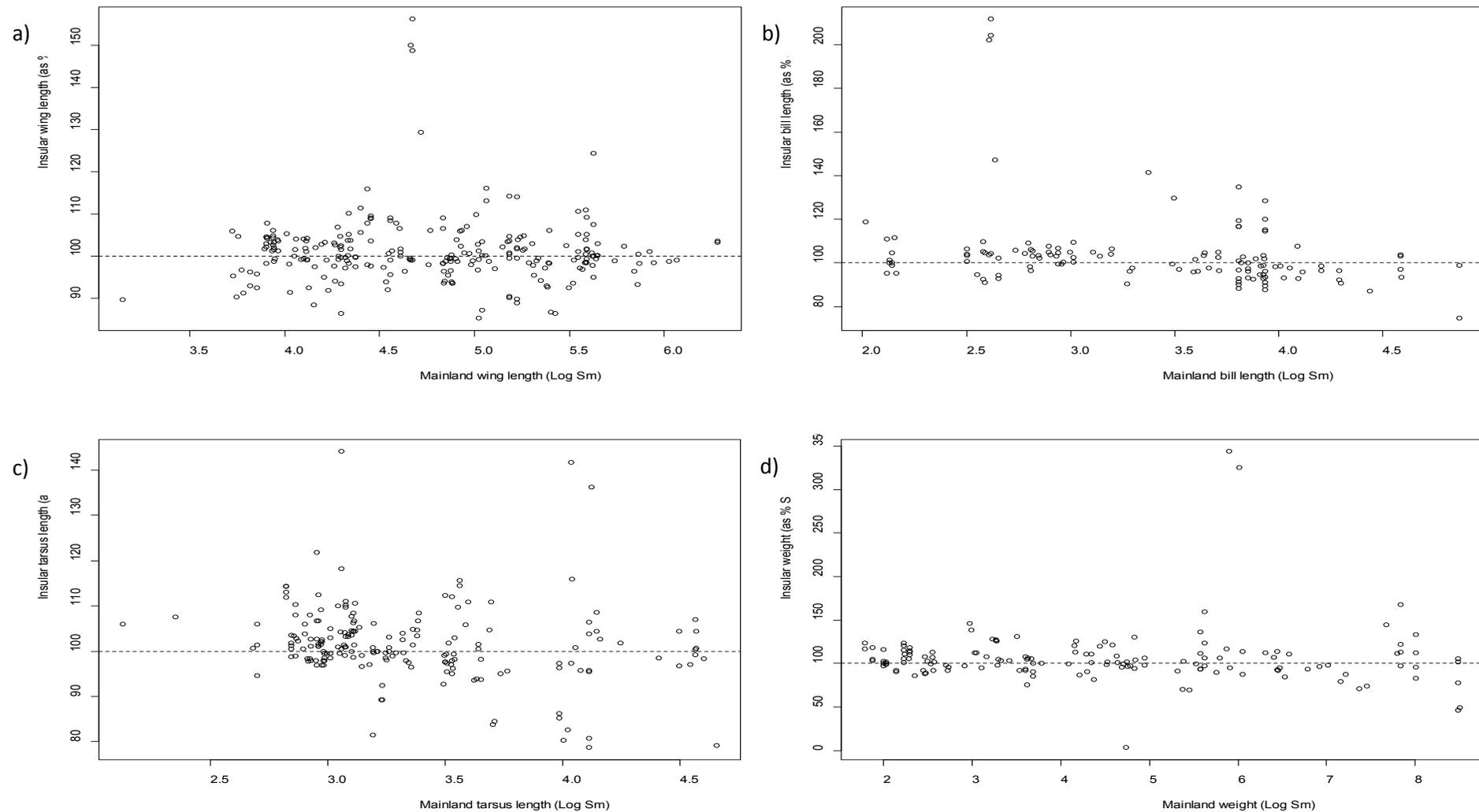


Figure 3.1 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a)wing (mm), b)bill (mm), c)tarsus (mm) and d)weight (grams) measurements, for all species combined at species level. Species above the 100% line show an insular body size increase while species below the same line show an insular body size decrease.

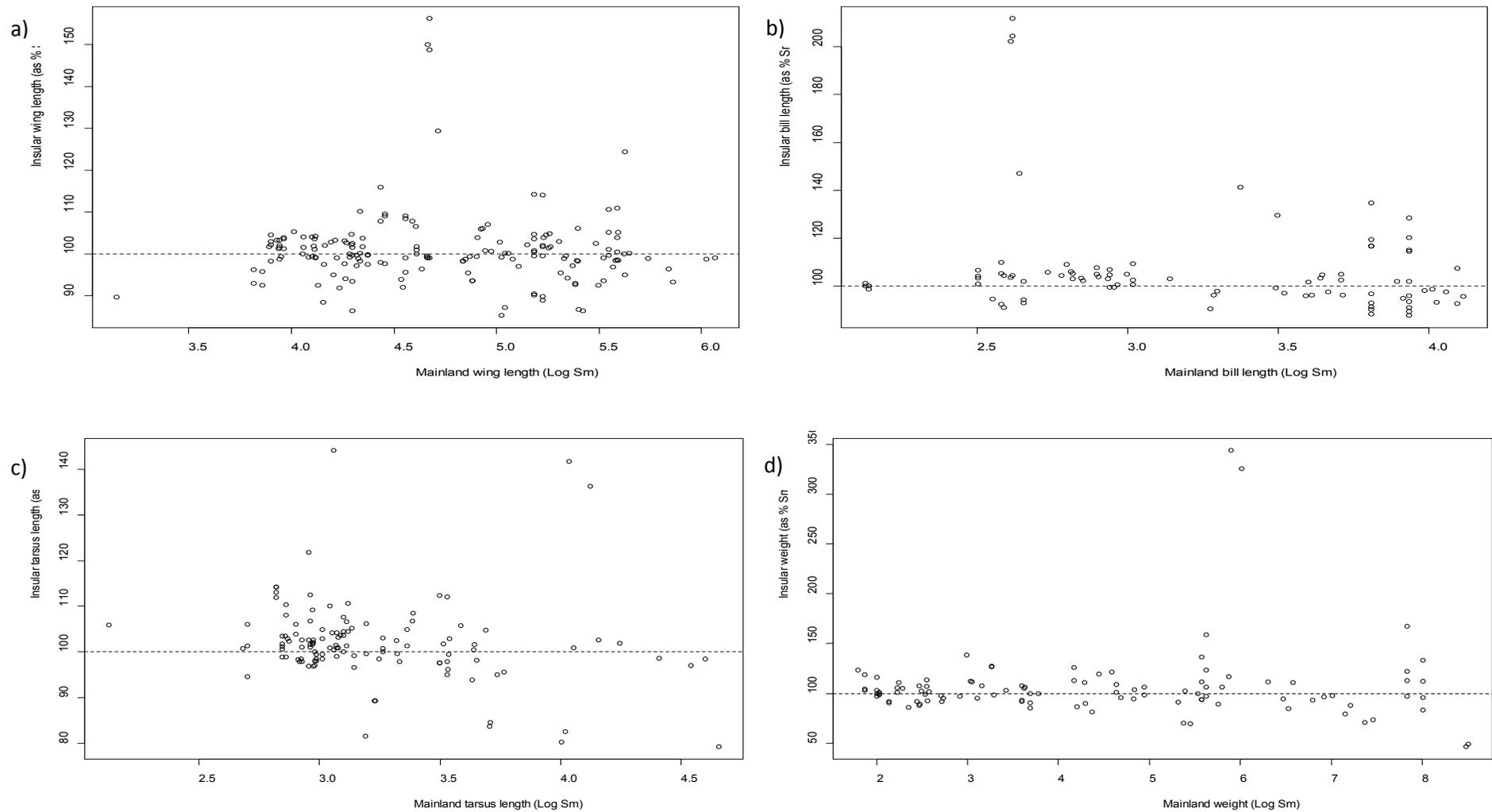


Figure 3.2 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a) wing (mm), b) bill (mm), c) tarsus (mm) and d) weight (grams) measurements, for small species at species level. Species above the 100% line show an insular body size increase while species below the same line show an insular body size decrease.

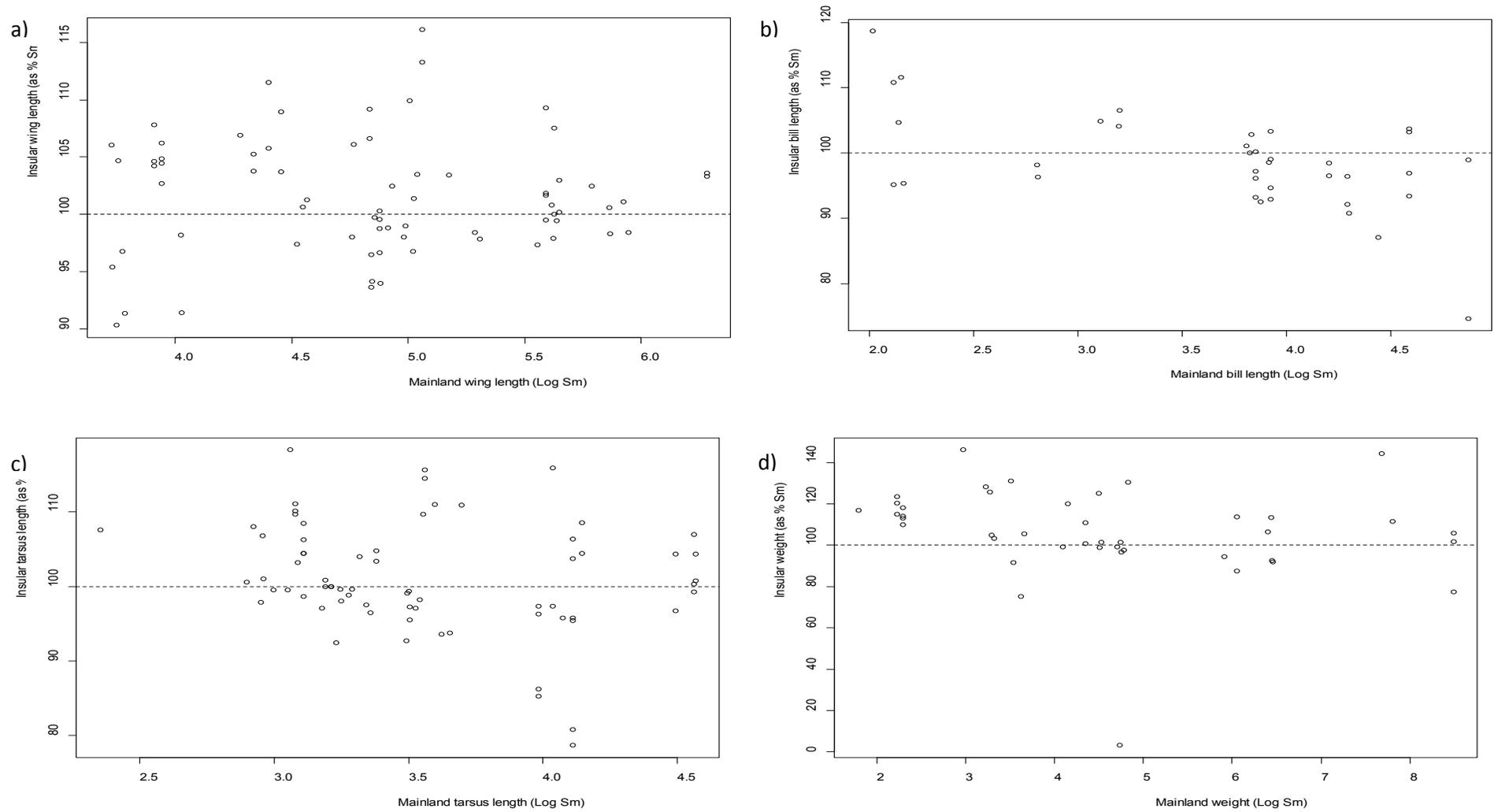


Figure 3.3 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a)wing (mm), b)bill (mm), c)tarsus (mm) and d)weight (grams) measurements, for large species at species level. Species above the 100% line show an insular body size increase while species below the same line show an insular body size decrease.

3.1.2 Order level

At the order level analyses for all combined species, there were significant differences between insular and mainland avian species for wing and tarsus length in the order Passeriformes (Table 3.4). Near significant differences were observed for wing (order Charadriiformes) and bill (order Procellariiformes) lengths. The obtained values for relative insular body size (i.e., SR) were very similar to one, showing no major trend for insular body size. Still, the ratio between insular and mainland birds implied a slight trend towards gigantism (i.e., $SR > 1$) in most of the orders for wing, bill and tarsus length at this level. Conversely, the values of SR indicated a weak trend towards a size reduction (i.e., $SR < 1$) in three of the four analysed orders for weight measurements.

The 'island rule' patterns were statistically confirmed with a slope of the regression of insular size on mainland size significantly less than 1 (Lomolino 1985) only for the wing length of the order Charadriiformes and the bill length of the orders Charadriiformes and Gruiformes (Table 3.4). But, because the obtained slopes were very close to one, only little size variation between traits from island and mainland birds can be recognized. It is important to mention that because multiple tests were performed on the same data, some of the statistically significant results could have been obtained by chance alone.

Table 3.4 Outcome of t-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at order level (n<10) for all species combined.

Trait	Order	n	t-test		SR	Regression Si against Sm (testing slope against 1)	
			t value	p value		Slope	p value
Wing	Charadriiformes	13	-1.83	0.093	1.055	0.75	0.010
	Passeriformes	137	-2.19	0.030	1.015	1.02	0.055
	Procellariiformes	18	0.30	0.767	1.012	1.10	0.008
	Psittaciformes	11	-1.21	0.255	1.017	0.90	0.170
	Sphenisciformes	14	0.38	0.710	0.995	0.89	0.805
Bill	Charadriiformes	14	-1.67	0.118	1.048	0.67	0.003
	Gruiformes	14	-0.42	0.684	0.999	0.62	0.001
	Passeriformes	24	-1.25	0.224	1.015	0.98	0.455
	Procellariiformes	17	-1.83	0.085	1.014	0.99	0.538
	Psittaciformes	11	-1.53	0.157	1.047	0.95	0.555
	Sphenisciformes	22	-0.84	0.410	1.034	1.05	0.852
Tarsus	Gruiformes	14	0.31	0.762	1.003	1.10	0.659
	Passeriformes	109	-4.36	0.000	1.026	0.99	0.531
	Procellariiformes	15	-0.81	0.434	1.015	1.01	0.661
Weight	Passeriformes	77	-0.12	0.905	1.007	0.93	0.120
	Procellariiformes	17	-0.65	0.528	0.976	1.00	0.854
	Psittaciformes	11	0.44	0.667	0.954	0.95	0.312
	Sphenisciformes	12	0.66	0.524	0.934	0.63	0.207

For the divided data, my analyses indicated significant differences between insular and mainland small birds only for bill (order Procellariiformes) and tarsus (order Passeriformes) lengths, as shown in Table 3.5. The ratio between insular and mainland birds indicated a slight trend towards gigantism (i.e., $SR > 1$) in most of the orders for the four studied traits. However, the 'island rule' patterns were confirmed by the regression of insular size on mainland size with a slope significantly less than 1 (Lomolino 1985) only for wing (order Charadriiformes), bill (order Charadriiformes), and tarsus (order Passeriformes) length (Table 3.5).

For large bird species, my analyses showed significant differences between insular and mainland large birds for wing (order Passeriformes), bill (order Gruiformes) and tarsus (order Gruiformes and Passeriformes) length, as shown in Table 3.6. The ratio between insular and mainland birds indicated, in a weak manner, the expected trend towards dwarfism (i.e., $SR < 1$) only in bill (order Gruiformes), tarsus (order Gruiformes), and weight (order Passeriformes) measurements. Nevertheless, the 'island rule' patterns were not corroborated by the regression of insular size on mainland size with a slope significantly less than 1 (Lomolino 1985) for any trait of any order (Table 3.6).

It is important to mention that because the obtained values for relative insular body size (i.e., SR) were very similar to one in both small- and large-bodied birds, the obtained trends towards dwarfism or gigantism were representing only minor patterns on insular body size variation. Similarly, all the obtained slopes from the regression of insular size on mainland size for both small and large birds performed to corroborate the 'island rule patterns' were close to one. This high similarity of the slopes to unity indicated a very small size variation between traits from island and mainland avifauna in both small and large birds. Also, some of the statistically significant results could have been obtained by chance alone because multiple tests were performed on the same data.

Table 3.5 Small species: Outcome of t-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at order level (n<10) for small species.

Trait	Order	n	t-test		SR	Regression Si against Sm (testing slope against 1)	
			t value	p value		Slope	p value
Wing	Charadriiformes	11	-1.86	0.093	1.068	0.75	0.027
	Passeriformes	86	-0.77	0.445	1.007	1.02	0.241
	Procellariiformes	14	0.12	0.904	1.010	1.21	0.007
	Sphenisciformes	14	0.38	0.710	0.995	0.09	0.805
Bill	Charadriiformes	12	-1.98	0.073	1.110	0.66	0.014
	Passeriformes	16	0.24	0.813	0.998	1.00	0.972
	Procellariiformes	12	-2.35	0.039	1.022	0.94	0.158
	Sphenisciformes	22	-0.84	0.410	1.034	1.05	0.852
Tarsus	Passeriformes	64	-2.96	0.004	1.020	0.93	0.036
Weight	Passeriformes	45	-1.99	0.053	1.053	1.02	0.389
	Procellariiformes	14	-0.98	0.344	1.133	1.09	0.052
	Sphenisciformes	12	0.66	0.524	0.934	0.63	0.207

Table 3.6 Large species: Outcome of t-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at order level (n<10) for large species.

Trait	Order	n	t-test		SR	Regression Si against Sm (testing slope against 1)	
			t value	p value		Slope	p value
Wing	Passeriformes	51	-2.47	0.017	1.024	1.01	0.376
Bill	Gruiformes	12	3.51	0.005	0.966	0.96	0.541
Tarsus	Gruiformes	12	2.59	0.025	0.948	1.24	0.035
	Passeriformes	45	-3.22	0.002	1.033	1.00	0.900
Weight	Passeriformes	32	0.27	0.788	0.992	0.88	0.217

For the combined data (Figure 3.4), the morphological shifts associated with the 'island rule' can only be recognized for wing length of the order Charadriiformes and the bill length of the orders Charadriiformes and Gruiformes. The resulting insular values for small values of these measurements for mainland species were above the 100% line, indicating a body size increment. For their large values, the corresponding insular values were below the 100% line, indicating a body size decrease.

After splitting the data, the morphological shifts dictated by the 'island rule' were recognized only for wing (order Charadriiformes) and bill (order Charadriiformes and Gruiformes) length of small-bodied birds (Figure 3.5), and a slight trend for bill (order Gruiformes) and weight (order Passeriformes) measurements of large-bodied birds (Figure 3.6). For small values of the mentioned measurements for mainland species, the corresponding insular values were above the 100% line, indicating a trend towards gigantism. For their large values, the corresponding insular values were below the 100% line, indicating a trend towards dwarfism.

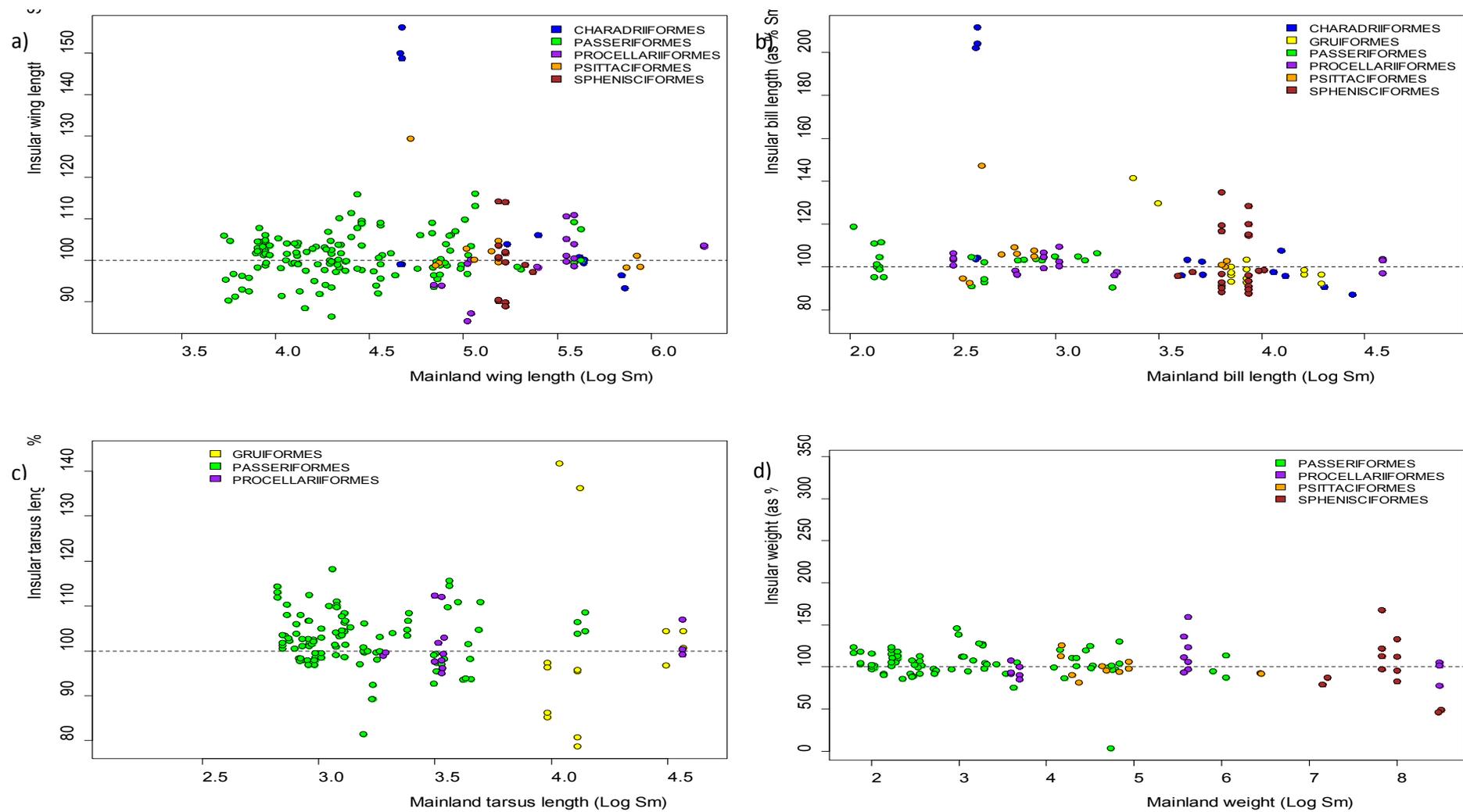


Figure 3.4 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a) wing (mm), b) bill (mm), c) tarsus (mm) and d) weight (grams) measurements for all species combined at order level. Orders above the 100% line show an insular body size increase while orders below the same line show an insular body size decrease.

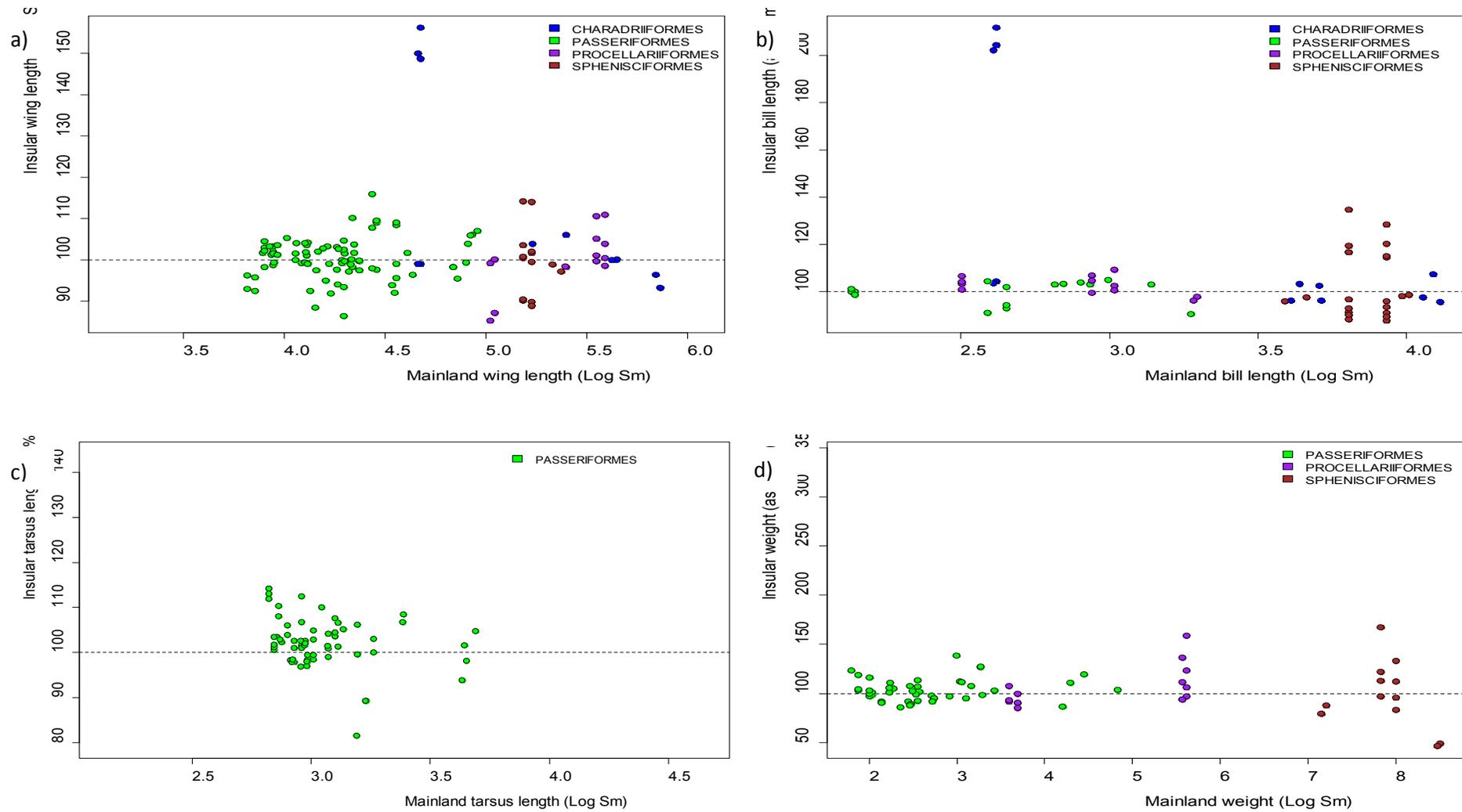


Figure 3.5 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a) wing (mm), b) bill (mm), c) tarsus (mm) and d) weight (grams) measurements, for small species at order level. Orders above the 100% line show an insular body size increase while orders below the same line show an insular body size decrease.

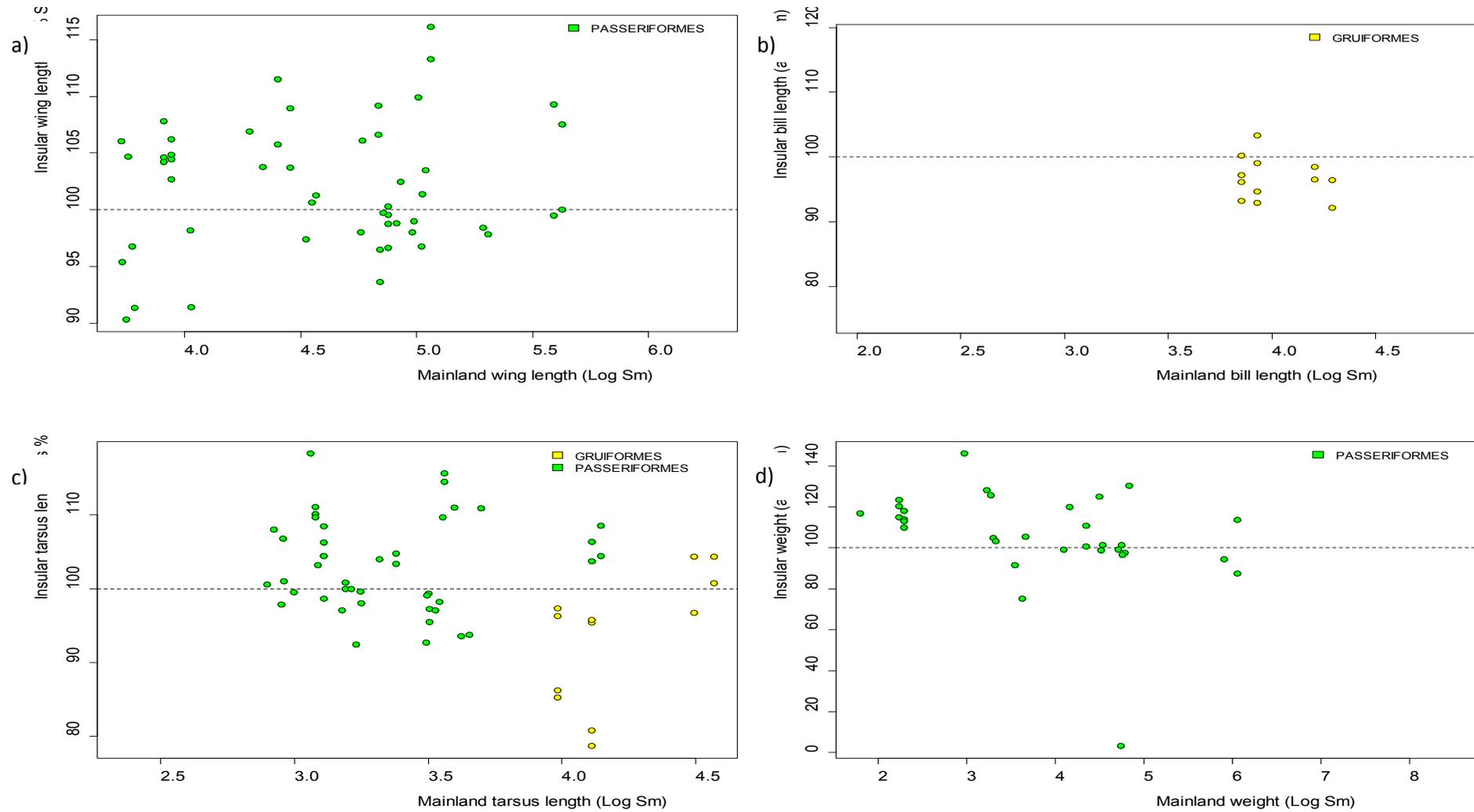


Figure 3.6 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for large species at order level. Orders above the 100% line show an insular body size increase while orders below the same line show an insular body size decrease.

3.1.3 Family level

At the family level, my analyses of the combined bird data resulted in significant differences between insular and mainland birds for wing (Meliphagidae and Procellariidae families), tarsus (Maluridae, Meliphagidae and Pardalotidae families), and weight (Pardalotidae family) measurements (Table 3.7). The ratio between insular and mainland birds implied a trend towards gigantism (i.e., $SR > 1$) in most of the families for wing, bill and tarsus length. Conversely, the values of this ratio indicate a size reduction (i.e., $SR < 1$) in almost all the analysed families for weight measurements. However, just like for the order level analyses, the obtained SR values were very similar to one, demonstrating only weak trends for insular body size.

The 'island rule' patterns were confirmed by a slope of the regression of insular size on mainland size significantly less than 1 (Lomolino 1985) only for the wing length of the Pardalotidae family and the bill length of the Rallidae family (Table 3.7). The assessment of the tarsus length data of the Petroicidae family also showed a consistency with the 'island rule' patterns, but did not reach statistical significance. Nevertheless, the obtained slopes were very similar to unity, so there were not major size variations between traits from island and mainland birds. Also, as indicated for the order level analyses, some of the statistically significant results could have been obtained by chance alone because multiple tests are performed on the same data.

Table 3.7 Outcome of t-test, SR (Si/Sm) and Regression Si against Sm (testing slope against 1) for wing length, bill length, tarsus length and weight at family level (n<10) for all species combined.

Trait	Order	Family	n	t-test		SR	Regression of Si against Sm (testing slope against 1)	
				t value	p value		Slope	p value
Wing	Passeriformes	Maluridae	17	0.23	0.819	1.001	1.39	0.032
		Meliphagidae	42	-2.78	0.008	1.036	1.09	0.002
		Pardalotidae	19	-1.43	0.170	1.012	0.72	0.021
	Procellariiformes	Procellariidae	12	-2.29	0.043	1.031	1.02	0.591
	Sphenisciformes	Spheniscidae	14	0.38	0.710	0.995	0.90	0.805
Bill	Passeriformes	Meliphagidae	14	-0.29	0.777	1.009	1.06	0.389
	Procellariiformes	Procellariidae	11	-1.50	0.165	1.015	0.99	0.564
	Gruiformes	Rallidae	14	-0.42	0.684	0.999	0.62	0.001
	Sphenisciformes	Spheniscidae	22	-0.84	0.410	1.034	1.05	0.852
Tarsus	Passeriformes	Maluridae	17	-2.87	0.011	1.037	1.37	0.021
		Meliphagidae	23	-4.93	0.000	1.058	1.07	0.063
		Pardalotidae	17	-4.07	0.001	1.037	1.10	0.373
		Petroicidae	11	0.32	0.754	0.984	0.84	0.081
	Procellariiformes	Procellariidae	11	-0.65	0.531	1.016	1.01	0.778
	Gruiformes	Rallidae	14	0.31	0.762	1.003	1.10	0.659
Weight	Passeriformes	Meliphagidae	21	0.74	0.468	0.962	0.73	0.196
		Pardalotidae	13	-2.94	0.012	1.057	0.87	0.158
	Procellariiformes	Procellariidae	11	-1.24	0.244	0.976	0.94	0.183
	Sphenisciformes	Spheniscidae	12	0.66	0.524	0.934	0.63	0.207

When differentiated by their size, there were significant differences between insular and mainland small species only for tarsus (Meliphagidae and Pardalotidae families) and weight (Pardalotidae family) measurements (Table 3.8). The ratio between insular and mainland body sizes implied the expected 'island rule' trend towards gigantism (i.e., $SR > 1$) in most of the families for the four studied traits. Nevertheless, the 'island rule' patterns were corroborated by the regression of insular size on mainland size with a slope significantly less than 1 (Lomolino 1985) only for the wing length of the Pardalotidae family (Table 3.8).

Similarly, there were significant differences between insular and mainland large bird species for bill (Rallidae family) and tarsus (Maluridae and Rallidae families) length, as shown in Table 3.9. The ratio between insular and mainland birds implies the expected 'island rule' trend towards dwarfism (i.e., $SR < 1$) only in bill and tarsus length of the Rallidae family. But, the 'island rule' patterns were not supported by the regression of insular size on mainland size with a slope significantly less than 1 for any of the studied traits for any family (Table 3.9). It is important to notice that the analyses could not be performed for the weight measurements of large birds because the sample size was not large enough.

Because the obtained SR values were very similar to one in both small- and large-bodied birds, the found trends towards dwarfism or gigantism were showing only weak patterns on insular body size variation. Likewise, all the obtained slopes from the regression of insular size on mainland size for both small and large birds were also very close to one. This high proximity of the slope to unity indicated a very small size variation between traits from island and mainland birds. As multiple tests were performed on the same data, some of the statistically significant results could have been obtained by chance alone.

Table 3.8 Outcome of *t*-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length, tarsus length and weight at family level (n<10) for small species.

Trait	Order	Family	n	t-test		SR	Regression of Si against Sm (testing slope against 1)	
				t value	p value		Slope	p value
Wing	Passeriformes	Meliphagidae	33	-1.27	0.213	1.016	1.07	0.223
		Pardalotidae	19	-1.43	0.170	1.012	0.72	0.021
	Sphenisciformes	Spheniscidae	14	0.38	0.710	0.995	0.90	0.805
Bill	Passeriformes	Meliphagidae	12	0.24	0.815	0.998	1.02	0.808
	Sphenisciformes	Spheniscidae	22	-0.84	0.410	1.034	1.05	0.852
Tarsus	Passeriformes	Meliphagidae	14	-3.30	0.006	1.032	0.90	0.168
		Pardalotidae	17	-4.07	0.001	1.037	1.10	0.373
Weight	Passeriformes	Meliphagidae	15	-0.43	0.676	1.029	1.06	0.417
		Pardalotidae	13	-2.94	0.012	1.057	0.87	0.158
	Sphenisciformes	Spheniscidae	12	0.66	0.524	0.934	0.63	0.207

Table 3.9 Outcome of *t*-test, relative insular body size (SR = insular size (Si)/ mainland size (Sm)) and regression of insular size (Si) against mainland size (Sm) (testing slope against 1) for wing length, bill length and tarsus length at family level (n<10) for large species. Not enough replications for analyses of weight measurements.

Trait	Order	Family	n	t-test		SR	Regression of Si against Sm (testing slope against 1)	
				t value	p value		Slope	p value
Wing	Passeriformes	Maluridae	13	-0.8	0.439	1.018	1.38	0.034
Bill	Gruiformes	Rallidae	12	3.51	0.005	0.966	0.96	0.541
Tarsus	Passeriformes	Maluridae	13	-4.37	0.001	1.054	1.27	0.064
	Gruiformes	Rallidae	12	2.59	0.025	0.948	1.24	0.035

As shown in Figure 3.7, the morphological shifts associated with the 'island rule' can be recognized in the undivided data only for wing (Pardalotidae family), bill (Procellariidae and Rallidae families), tarsus (Petroicidae family) and weight measurements (Pardalotidae and Procellariidae families). The resulting insular values for small values of these measurements for mainland species were above the 100% line, indicating a body size increase. On the contrary, for their large values, the corresponding insular values were below the 100% line, indicating a body size decrease (Figure 3.7).

For the divided data, the morphological shifts dictated by the 'island rule' can be recognized in small species (Figure 3.8) only for wing (Pardalotidae family), bill (Meliphagidae family), tarsus (Meliphagidae family), and weight measurements (Pardalotidae family). Similarly, the 'island rule' pattern can be identified in large species (Figure 3.9) only for bill (Rallidae family) and tarsus length (Maluridae and Rallidae families). For small values of the mentioned measurements for mainland species, the corresponding insular values were above the 100% line, indicating a trend towards body size enlargement. In opposition, for their large values, the corresponding insular values were below the 100% line, indicating a trend towards body size shrinkage.

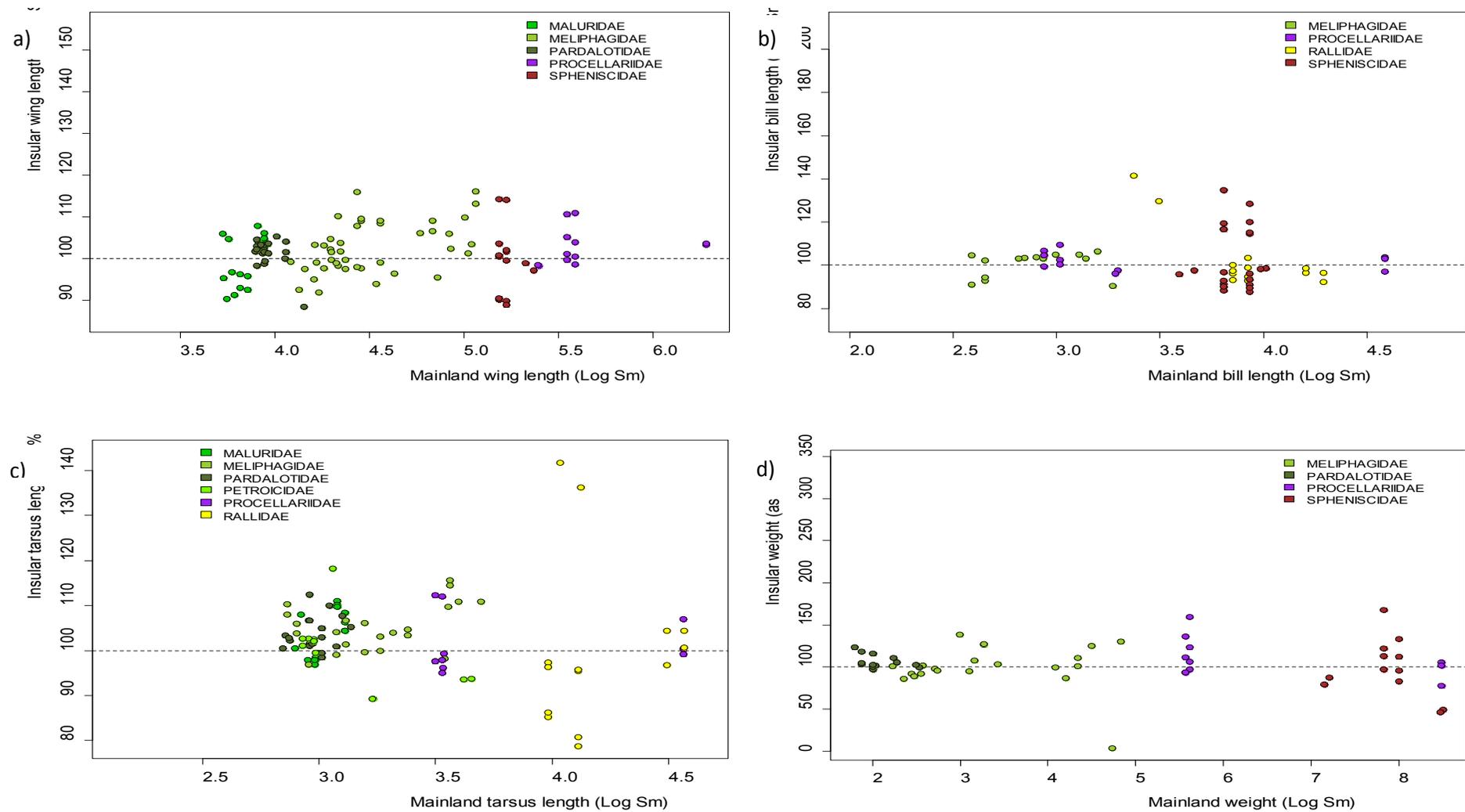


Figure 3.7 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a)wing (mm), b)bill (mm), c)tarsus (mm) and d)weight (grams) measurements for all species combined at family level. Families above the 100% line show an insular body size increase while families below the same line show an insular body size decrease.

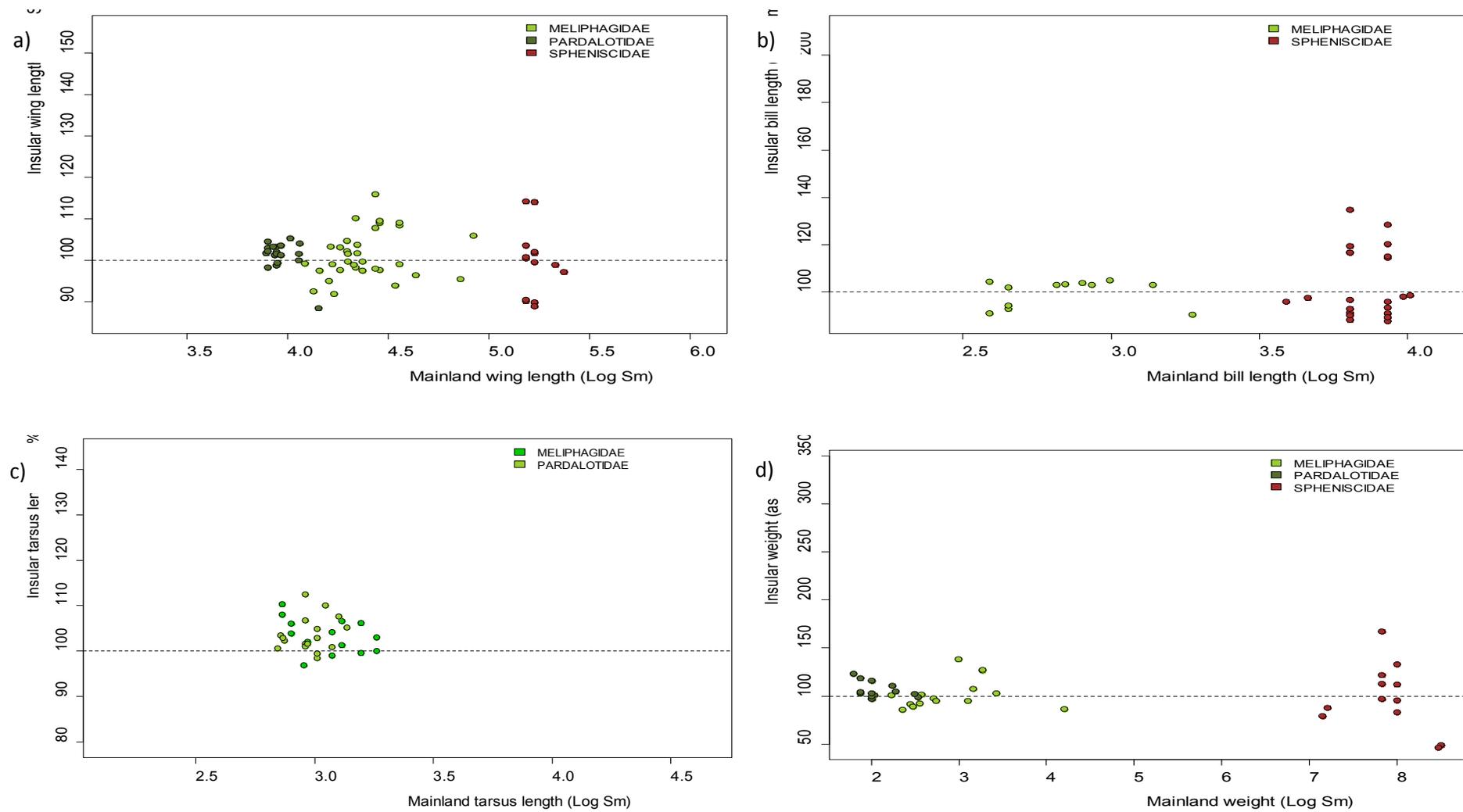


Figure 3.8 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a) wing (mm), b) bill (mm), c) tarsus (mm) and d) weight (grams) measurements, for small species at family level. Families above the 100% line show an insular body size increase while families below the same line show an insular body size decrease.

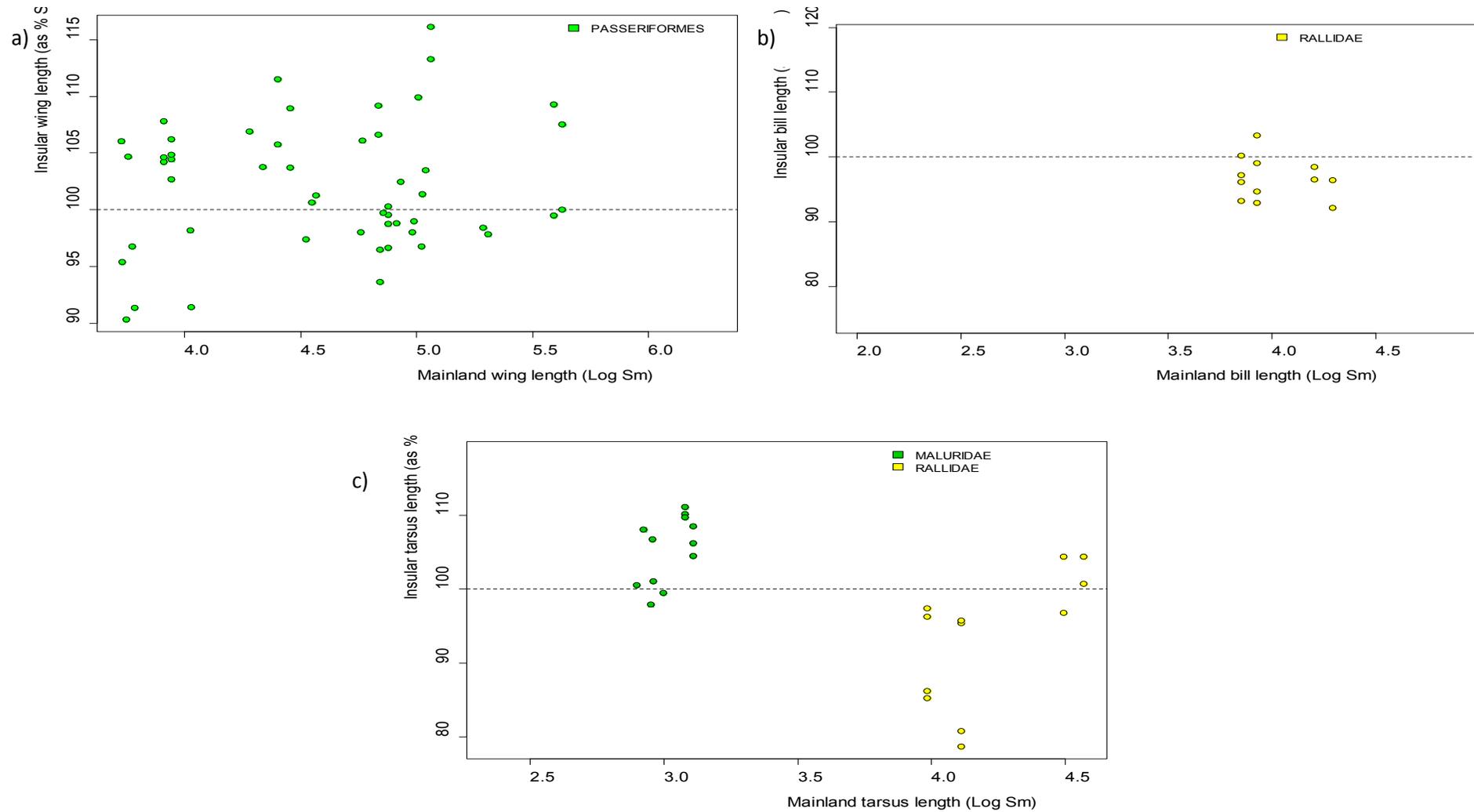


Figure 3.9 Regression of Log mainland measurement (Log Sm) on Log insular measurement (as percentage of mainland measurement, Log Si as % of Sm) for a)wing (mm), b)bill (mm), and c)tarsus (mm) measurements, for large species at family level. Families above the 100% line show an insular body size increase while families below the same line show an insular body size decrease.

3.2 Objective 2: Comparing the degree of sexual size dimorphisms between insular and mainland birds

Contrary to my third hypothesis regarding sexual size dimorphism, I did not find enough statistical support to indicate that the insular SSDs were consistently greater than mainland SSDs. At the species and family level, my analysis did not find significant evidence of a bigger insular SSD for any of the traits in the combined or split datasets (Tables 3.10, 3.11, 3.12, 3.13, 3.14, and 3.15). The *t*-test could not be performed for the weight measurements of the large data at the family level because of the lack of enough replications (less than five comparisons within each family). Still, at the order level I found that insular SSD was significantly more divergent than mainland SSD for weight measurements of the order Procellariiformes when both the combined and small bird datasets, but not the large bird datasets, were assessed (Tables 3.16, 3.17 and 3.18).

Table 3.10 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (H_i: SSDm<SSDi) for all species combined, at the species level.

Trait	n	<i>t</i> -test	
		t value	p value
Wing	102	1.455	0.926
Bill	54	0.018	0.507
Tarsus	78	1.229	0.889
Weight	57	-0.269	0.395

Table 3.11 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (H_i: SSDm<SSDi) for small species, at the species level.

Trait	n	<i>t</i> -test	
		t value	p value
Wing	74	1.847	0.966
Bill	40	1.599	0.941
Tarsus	51	0.628	0.734
Weight	43	-0.413	0.341

Table 3.12 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (H_i: SSDm<SSDi) for large species, at the species level.

Trait	n	<i>t</i> -test	
		t value	p value
Wing	28	0.016	0.506
Bill	14	-0.960	0.177
Tarsus	27	1.197	0.879
Weight	14	0.144	0.556

Table 3.13 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for all species combined, at the order level.

Trait	Order	n	<i>t</i> -test	
			t value	p value
Wing	Passeriformes	58	0.70	0.755
	Procellariiformes	8	1.68	0.931
	Sphenisciformes	7	2.03	0.955
Bill	Charadriiformes	6	-0.94	0.196
	Gruiformes	7	1.13	0.849
	Passeriformes	11	0.23	0.589
	Procellariiformes	7	0.05	0.519
	Sphenisciformes	11	1.16	0.864
Tarsus	Gruiformes	7	1.57	0.916
	Passeriformes	45	0.49	0.687
	Procellariiformes	6	0.24	0.592
Weight	Passeriformes	26	1.82	0.960
	Procellariiformes	7	-4.73	0.002
	Sphenisciformes	6	1.28	0.872

Table 3.14 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for small species, at the order level.

Trait	Order	n	<i>t</i> -test	
			t value	p value
Wing	Passeriformes	37	0.87	0.804
	Procellariiformes	7	1.80	0.939
	Sphenisciformes	7	2.03	0.955
Bill	Passeriformes	7	0.85	0.787
	Procellariiformes	6	0.40	0.646
	Sphenisciformes	11	1.16	0.864
Tarsus	Passeriformes	27	0.07	0.529
Weight	Passeriformes	15	1.64	0.939
	Procellariiformes	7	-4.73	0.002
	Sphenisciformes	6	1.28	0.872

Table 3.15 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for large species, at the order level.

Trait	Order	n	<i>t</i> -test	
			t value	p value
Wing	Passeriformes	21	0.10	0.538
Bill	Gruiformes	6	0.49	0.678
Tarsus	Gruiformes	6	1.21	0.859
	Passeriformes	18	0.69	0.750
Weight	Passeriformes	11	1.00	0.831

Table 3.16 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for all species combined, at the family level.

Trait	Order	Family	n	t-test	
				t value	p value
Wing	Passeriformes	Maluridae	8	0.23	0.586
		Meliphagidae	18	0.34	0.630
		Pardalotidae	7	0.93	0.806
	Sphenisciformes	Spheniscidae	7	2.03	0.955
Bill	Passeriformes	Meliphagidae	6	0.00	0.499
	Gruiformes	Rallidae	7	1.13	0.849
	Sphenisciformes	Spheniscidae	11	1.16	0.864
Tarsus	Passeriformes	Maluridae	8	2.30	0.973
		Meliphagidae	9	-0.98	0.178
		Pardalotidae	7	2.23	0.966
	Gruiformes	Rallidae	7	1.57	0.916
Weight	Passeriformes	Meliphagidae	8	0.19	0.573
	Sphenisciformes	Spheniscidae	6	1.28	0.872

Table 3.17 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for small species, at the family level.

Trait	Order	Family	n	t-test	
				t value	p value
Wing	Passeriformes	Meliphagidae	15	1.21	0.877
		Pardalotidae	7	0.93	0.806
	Sphenisciformes	Spheniscidae	7	2.03	0.955
Bill	Sphenisciformes	Spheniscidae	11	1.16	0.864
Tarsus	Passeriformes	Meliphagidae	6	-0.40	0.354
		Pardalotidae	7	2.23	0.966
Weight	Passeriformes	Meliphagidae	6	1.33	0.880
	Sphenisciformes	Spheniscidae	6	1.28	0.872

Table 3.18 Outcome for *t*-test between the sexual size dimorphism ratio of mainland (SSDm) and island (SSDi) species (Hi: SSDm<SSDi) for large species, at the family level. Not enough replications for analyses of weight measurements.

Trait	Order	Family	n	t-test	
				t value	p value
Wing	Passeriformes	Maluridae	6	-0.08	0.469
Bill	Sphenisciformes	Spheniscidae	6	0.49	0.678
Tarsus	Passeriformes	Maluridae	6	3.60	0.922
	Gruiformes	Rallidae	6	1.21	0.859

3.3 Objective 3: Testing the effect of moderators on avian insular morphological shifts

Mean relative insular body sizes were calculated for each trait as the natural base exponential of the mean effect sizes obtained by the meta-analyses (i.e., $SR = (\text{mean effect size})^e$) for the combined, small- and large-bodied datasets. Overall, the obtained SR values for the three datasets were very close to unity, so no strong insular body size patterns can be inferred for any trait. For all species combined, the mean SR values for the four studied traits reflected a general but weak tendency for bird species to become larger on islands ($SR > 1$; Table 3.19). However, these outcomes were significant only for bill and tarsus length.

When split on the basis of species' body size, SR values for both small and large species indicated a common but slight tendency towards gigantism ($SR > 1$; Table 3.20). However, these results were only significant for bill length in small species (Table 3.20). In the case of wings of the small-bodied birds, the resulting mean SR was equal to 1, reflecting a lack of insular body size change. Conversely, for large species only bill length expressed a slight trend towards dwarfism ($SR < 1$), but it was not statistically significant (Table 3.20). For all the other large species traits, SR was slightly greater than 1, indicating a minor increase in insular size that was statistically significant for wings and weights measurements (Table 3.20).

The heterogeneity test values (Q) for each resulting mean effect size were calculated for both analyses of the combined and split datasets (Tables 3.19 and 3.20). Q was significant for all the obtained mean effect sizes, which means that the analysed studies did not share the same effect size. Therefore, heterogeneity exists between them and it is not caused only by sampling errors. It is important to indicate that for the weight measurements of the combined and large species data I was not able to use the multivariate models like in all of the other traits because of the lack of replications across the random effects, so I tested meta-analytic models using the 'rma' function.

Table 3.19 Results from the meta-analysis using the 'rma.mv' function (except for weights where 'rma' function without random-effects argument was used) for all species combined. SR and its confidence interval (CI) were calculated as the natural base exponential of the estimate and its CI.

Trait	n	mean effect size	mean effect size CI		SR	SR CI		P value estimate	Test for Heterogeneity (Q)	P value Q test
			lower bound	upper bound		lower bound	upper bound			
Wing	242	0.01	-0.0041	0.0206	1.01	0.9959	1.0208	0.188	18114.47	<0.0001
Bill	125	0.04	0.0015	0.0705	1.04	1.0015	1.0730	0.041	9568.90	<0.0001
Tarsus	190	0.02	0.0007	0.0327	1.02	1.0007	1.0332	0.041	9202.12	<0.0001
Weight	146	0.04	-0.0010	0.0722	1.04	0.9990	1.0749	0.057	11312461.92	<0.0001

Table 3.20 Results from the meta-analysis using the 'rma.mv' function (except for large species weights where 'rma' function without random-effects argument was used) for small and large species. SR and its confidence interval (CI) were calculated as the natural base exponential of the estimate and its CI.

Trait	size	n	mean effect size	mean effect size CI		SR	SR CI		P value estimate	Test for Heterogeneity (Q)	P value Q test
				lower bound	upper bound		lower bound	upper bound			
Wing	small	172	0.00	-0.0115	0.0211	1.00	0.9886	1.0213	0.563	16157.02	<0.0001
	large	70	0.02	0.0006	0.0319	1.02	1.0006	1.0324	0.042	1436.22	<0.0001
Bill	small	89	0.06	0.0127	0.1044	1.06	1.0128	1.1100	0.012	8613.96	<0.0001
	large	36	-0.02	-0.0510	0.0201	0.98	0.9503	1.0203	0.395	759.65	<0.0001
Tarsus	small	121	0.02	-0.0050	0.0379	1.02	0.9950	1.0386	0.134	6494.37	<0.0001
	large	69	0.02	-0.0066	0.0411	1.02	0.9934	1.0420	0.156	2705.83	<0.0001
Weight	small	104	0.03	-0.0287	0.0834	1.03	0.9717	1.0870	0.339	5015.27	<0.0001
	large	42	0.07	0.0226	0.1161	1.07	1.0229	1.1231	0.004	11306949.88	<0.0001

The AICc comparisons from the meta-analyses models showed that the small and the combined species datasets had the same best model for each trait (Tables 3.21 and 3.22, correspondingly): the full model for wing and weight measurements, sea surface temperature model for bill lengths and distance from mainland model for tarsus lengths. Most of these models were clearly distinguished because they were more than two AICc points different from each other. They were also many AICc points away from their correspondingly null models, indicating that they were explaining a substantial amount of the little variation in the mean SR. For the weight measurements from the combined species dataset, the first and second best model (the full and distance from mainland models, respectively) were separated by less than two AICc points, so it is not possible to be certain about which model is best (Table 3.21). Similarly, because they were separated from the null model by merely two AICc points, it is not certain that these models explain any variation in the mean SR.

For the large species dataset, the comparisons of the AICc values showed that the sea surface temperature model was clearly the best model for wing length (Table 3.23). However, for the other three traits, the best resulting models were within two AICc points of the null model showing that these moderators were not important for variations in the mean SR.

The heterogeneity test values for the error (QE) were significant for all the fitted models. These significant values indicate that there is substantial unexplained variation that could not be accounted for in every tested model. However, as the observed SR values were very close to unity, very little variation could have been actually modelled by these explanatory models.

Table 3.21 Resulting Akaike information criterion corrected for finite samples sizes (AICc) values for the fitted models per trait for all species combined and heterogeneity test values for the error (QE).

Trait	Models	AICc	QE	QE p value
Wing	full	201.30	17731.56	<0.0001
	distance from mainland	204.44	17864.14	<0.0001
	island area	344.68	18050.34	<0.0001
	sea surface temperature	378.21	17980.24	<0.0001
	null	407.82	18114.47	<0.0001
Bill	sea surface temperature	-171.54	9547.78	<0.0001
	full	-162.27	9491.67	<0.0001
	null	-76.68	9568.89	<0.0001
	island area	-74.49	9568.86	<0.0001
	distance from mainland	-69.77	9567.96	<0.0001
Tarsus	distance from mainland	-85.87	8778.50	<0.0001
	full	-76.87	8484.67	<0.0001
	null	-61.82	9202.12	<0.0001
	island area	-60.21	9202.11	<0.0001
	sea surface temperature	-58.05	9180.96	<0.0001
Weight	full	14.08	175102.44	<0.0001
	distance from mainland	15.13	1807303.55	<0.0001
	null	16.46	11312461.92	<0.0001
	sea surface temperature	18.27	3175989.79	<0.0001
	island area	18.85	11310601.66	<0.0001

Table 3.22 Resulting Akaike information criterion corrected for finite samples sizes (AICc) values for the fitted models per trait for small species and heterogeneity test values for the error (QE)

Trait	Models	AICc	QE	QE p value
Wing	full	271.38	15946.41	<0.0001
	distance from mainland	297.84	16080.86	<0.0001
	island area	536.01	16143.29	<0.0001
	sea surface temperature	572.83	16030.86	<0.0001
	null	629.82	16157.02	<0.0001
Bill	sea surface temperature	-207.95	8539.46	<0.0001
	full	-198.18	8462.61	<0.0001
	null	-77.67	8613.96	<0.0001
	island area	-74.17	8564.76	<0.0001
	distance from mainland	-70.93	8531.58	<0.0001
Tarsus	distance from mainland	-202.39	5814.72	<0.0001
	full	-196.53	5427.20	<0.0001
	sea surface temperature	-163.47	6368.51	<0.0001
	null	-155.27	6494.37	<0.0001
	island area	-150.35	6470.68	<0.0001
Weight	full	779.20	4811.43	<0.0001
	sea surface temperature	783.44	4977.38	<0.0001
	distance from mainland	941.48	4900.92	<0.0001
	null	1246.86	5015.27	<0.0001
	island area	1250.20	4957.57	<0.0001

Table 3.23 Resulting Akaike information criterion corrected for finite samples sizes (AICc) values for the fitted models per trait for large species and heterogeneity test values for the error (QE).

Trait	Models	AICc	QE	QE p value
Wing	sea surface temperature	-226.59	1428.79	<0.0001
	null	-222.73	1436.22	<0.0001
	full	-220.69	1419.60	<0.0001
	distance from mainland	-218.07	1436.16	<0.0001
	island area	-215.50	1429.80	<0.0001
Bill	null	-3.0933	759.6458	<0.0001
	island area	1.538	724.0179	<0.0001
	sea surface temperature	3.0443	754.1501	<0.0001
	distance from mainland	3.7348	745.151	<0.0001
	full	14.1388	688.8767	<0.0001
Tarsus	null	101.19	2705.83	<0.0001
	island area	101.91	2653.14	<0.0001
	sea surface temperature	104.34	2610.30	<0.0001
	distance from mainland	105.28	2701.51	<0.0001
	full	108.75	2581.32	<0.0001
Weight	null	5.3505	11306949.88	<0.0001
	island area	8.4905	11300657.68	<0.0001
	sea surface temperature	8.3424	3159861.37	<0.0001
	distance from mainland	9.1338	1800903.353	<0.0001
	full	13.1937	49457.8653	<0.001

Using meta-analysis modelling, I calculated the estimates and their respective confidence intervals for the best model for each trait for each dataset. For the combined dataset, variation in SRs based on wing and weight measurements were significantly moderated by island area, distance from mainland and sea surface temperature (Table 3.24). Estimates showed that in all cases, except for distance from mainland and sea surface temperature in the model for weight, that the SR was positively related to the moderators. Variation in SRs based on bill and tarsus lengths were significantly explained by sea surface temperature and distance from mainland, respectively (Table 3.24).

Similarly, for the small-bodied birds' dataset, variation in SRs based on wing and weight measurements were significantly explained by the three tested explanatory variables (Table 3.25). Estimates indicated that in all cases, except for sea surface temperature in the full model for weight, the SR was positively related to the moderators. Variation in SRs based on bill and tarsus lengths were significantly explained by sea surface temperature and distance from mainland, respectively. Furthermore, the confidence intervals for the intercepts in the selected models for weight measurements indicated that the distance from mainland had poor predictive power (Table 3.25). On the other hand, for the large-bodied bird dataset, the null models were the top models for all the traits, except for wing lengths (Table 3.26). SR variation based on this last trait showed to be significantly negatively correlated to sea surface temperature.

Table 3.24 Estimates and their confidence intervals for best model based (lowest AICCc value) per trait for all species combined.

Trait	best model	model results	estimate	ci.lb	ci.ub
Wing	full model	island area	0.0100	0.0012	0.0122
		distance from mainland	0.0200	0.0133	0.0200
		sea surface temperature	0.0200	0.0080	0.0249
Bill	sea surface temperature model	sea surface temperature	0.0500	0.0411	0.0609
Tarsus	distance from mainland model	distance from mainland	0.0200	0.0121	0.0253
Weight	full model	island area	0.0461	0.0068	0.0853
		distance from mainland	-0.0599	-0.0982	-0.0216
		sea surface temperature	-0.0441	-0.0822	-0.0060

Table 3.25 Estimates and their confidence intervals for best model based (lowest AICCc value) per trait for small species.

Trait	best model	model results	estimate	ci.lb	ci.ub
Wing	full model	island area	0.0200	0.0098	0.0224
		distance from mainland	0.0200	0.0204	0.0280
		sea surface temperature	0.0300	0.0185	0.0392
Bill	sea surface temperature model	sea surface temperature	0.0700	0.0580	0.0813
Tarsus	distance from mainland model	distance from mainland	0.0400	0.0319	0.0543
Weight	full model	island area	0.0700	0.0211	0.1125
		distance from mainland	0.0200	-0.0273	0.0635
		sea surface temperature	-0.5098	-0.5865	-0.4331

Table 3.26 Estimates and their confidence intervals for best model based (lowest AICCc value) per trait for large species.

Trait	best model	model results	estimate	ci.lb	ci.ub
Wing	sea surface temperature model	sea surface temperature	-0.0200	-0.0393	-0.0100

Overall, none of findings show consistent support for the four hypotheses formulated for my study. Therefore, the 'island rule' morphological patterns cannot be sustained for the avifauna of the ANZA region.

Chapter 4

Discussion

The overall aim of this thesis was to identify and explain trends in the morphological variation of insular birds from the Australian, New Zealand and Antarctic region in order to test the validity of the 'island rule'. The expected expression of this rule is a tendency towards gigantism in small insular species and one towards dwarfism in large species that would be more obvious in smaller isolated islands (Foster 1964; Van Valen 1973a; Lomolino 1985; Clegg & Owens 2002; Lomolino 2005). Likewise, greater insular sexual size dimorphism were anticipated, with larger size variations between male and female insular bird species than their mainland forms, influenced by the physical and environmental characteristics of each island (Soule & Stewart 1970; Willson et al. 1975; Cook et al. 2013; Greenberg & Danner 2013; Luther & Greenberg 2014). In general, the estimated relative insular body size (SR) values for all the traits from all the datasets at all the assessed levels were very close to unity, indicating very minor and inconsistent insular body size variations. Therefore, my findings did not support the anticipated patterns dictated to the 'island rule' and, in fact, sometimes they were slightly opposite to the expected trends.

4.1 Insular body size

As a whole, there was some signal for a morphological trend associated with the 'island rule' for bill and tarsus length, which supported earlier studies on body size evolution of island birds (Grant 1965, 1968; Blondel 2000; Clegg & Owens 2002). There were inconsistent differences between insular and mainland birds at the species, family or order level. When all the species were analysed together, I found significant but slight differences for wing, bill and tarsus length, but not for weight. As these results may be affected by the great range of values within the data of each trait, I re-analysed the data separated into small-bodied and large-bodied birds groups according to the mean body length of their respective families. For these datasets I obtained weak differences; however, not always with statistical significance for bill and tarsus length. Therefore, my findings only indicate slight and inconsistent differences between insular and mainland avian body size based on bill and tarsus length.

According to early studies in avian body size evolution on islands, bill and tarsus morphology displays more variation than other traits on insular habitats because of the greater range of food resources that birds are exposed to (Grant 1965, 1968; Keast 1970; Case 1978). The link between insular morphological variations and food resources was supported by Clegg and Owens (2002) and Lomolino (2005), who also corroborated the 'island rule' patterns for bill and concluded that changes

in insular bill length were a response to changes in feeding ecology and reflected an adaptation towards generalism in a new scenario lacking of other species with similar needs (i.e., interspecific competition) or that represent a threat (e.g., predators). Additionally, Greenberg et al. (2012) stated that loss of heating and water conservation capacities may play a decisive role in the evolution of bill size on islands, and later studies by the same group of researches stressed the key role of the variations in bill morphology in thermal ecology of insular birds (Greenberg & Danner 2012, 2013). Nonetheless, more than 80% of the analysed data came from islands higher than latitude 30, where the temperature does not push birds to develop dissipation of heat strategies (Clegg & Owens 2002; Cassey & Blackburn 2004). On the other hand, tarsus length evolution on islands has been related to food and spatial resources as these structures are used by birds to perch while feeding and this change would let them search more efficiently for food (Grant 1965, 1971; Abbott 1980). The insular morphological shifts on these two traits would be a result of a combination of phenotypic plasticity, non-adaptive evolution and adaptive evolution (Clegg et al. 2002; Mathys & Lockwood 2011). According to McNab (2002) and Millien (2006), the insular morphological evolution would happen in accelerated periods, sometimes shorter than 150 years. However, more recent studies affirm that size evolution on islands would not be faster than on mainland (Raia & Meiri 2011).

The calculated relative insular body sizes (SR) exhibit an overall weak trend towards insular gigantism in small species whereas the 'island rule' pattern was even weaker for insular dwarfism in large species at the three analysed levels (i.e., species, family and order). All the obtained SRs for the four traits from all the datasets at the three assessed levels had values very similar to one, indicating only slight trends on insular body size variation. Regressing the insular relative body size on mainland body size (Lomolino 1985) found that only bill and tarsus significantly followed the 'island rule' pattern only for the combined and divided data. Lomolino et al. (2010) claimed that the 'island rule' pattern would be found at all taxonomic levels as phylogeny has a vital influence on insular body size evolution. However, the slim trend found for these two traits was not present at the family and order levels. Moreover, all the resulting slopes from this regression were also very close to one demonstrating very small size variation between traits from island and mainland birds. Also, as multiple tests were performed on the same data, some of the statistically significant results could have been obtained by chance alone. Multiple testing problems increase the chances of finding false positives and are commonly corrected by reducing the critical value of the *p value* using the Bonferroni or the Dunn–Sidak methods (Dytham 2011). Nevertheless, these corrections increase the possibility of a type II error (i.e. rejecting the null hypothesis when it is in fact true), so not making adjustments on biological data leads to better interpretations (Rothman 1990). For all these reasons, a confirmation of the morphological patterns associated with the 'island rule' was not supported. As a matter of fact, the 'island rule' pattern was neither recognized for the Passeriformes order,

contrary to what was found in previous studies (Grant 1965; Robinson-Wolrath & Owens 2003; Scott et al. 2003; Lomolino 2005; Luther & Greenberg 2011). My results show an overall slight enlargement in the species within this group on islands regardless their body size (see Tables 3.7, 3.8, and 3.9).

A possible explanation for the lack of prevalence of trends at higher taxonomic levels could be the low number of data points within each family and order. Also, considering that the assessed mainland/island species pairs were only from birds within the ANZA region, it is possible that these 'optimal' pairs were not distant enough chronologically and/or geographically to display stronger and more consistent patterns. Despite the fact that evolution is thought to take place on a different time scale on islands than on mainland (Millien 2006), the species forming the studied pairs may have not yet had time to express consistent divergence although distances between mainland and islands ranged up to 2800 km. Likewise, even though spatially close populations have shown dramatic differences in body size (Jessop et al. 2006), it is possible that the mean values for the traits of the evaluated mainland-island bird species pairs within the ANZA region did not include the extreme sizes of the traits for each species. If related species that were further apart in time and space were assessed then perhaps stronger patterns would have been shown, as in past global studies (Clegg & Owens 2002; Lomolino 2005; Meiri et al. 2008). Still, the assessed species pairs were from across the phylogenetic spectrum for birds registered in the region (Christidis & Boles 2008), so it should be representing a reasonable sample. My results are similar to those obtained by Meiri et al. (2008) for mammals, where they did not find enough support to conclude the generality of the 'island rule' pattern in all mammalian clades.

By performing meta-analyses I expected to recognize some patterns that were not clearly obtained by the more traditional statistical analyses. Overall, the resulting mean SRs in the performed meta-analyses (i.e., natural exponential of the estimate effect size) were also very close to unity, reflecting only weak tendencies for birds to become larger on islands regardless of whether their mainland counterparts were small- or large-bodied. When not accounting for their size, the mean SRs were greater than one for the four traits, but this body size enlargement had statistical significance only for bill and tarsus length. As these mean SRs could have been affected by the wide range of values for each trait, I repeated the meta-analyses after splitting the dataset by the birds' body length. In this assessment, the gigantism trends were significant only for bill length of small birds and wings and weight measurements of large birds. Still, the obtained SRs were very similar to one too, so the found body size enlargement trends resembling one of the body size patterns dictated by the 'island rule' were very slight. The test of heterogeneity values (Q) were significant for all the obtained effect sizes, indicating that the obtained SR values were more heterogeneous than expected by chance. As these SRs were calculated accounting for the random differences among studies, the heterogeneity was due to known and unknown moderators. But, because of the high

proximity of the SR values to unity, this heterogeneity was also very small. Therefore, meta-regression analyses including moderators that could further explain this little amount of variation in SR values were later performed.

Cassey and Blackburn (2004) also found that only the first half of the 'island rule' (i.e., enlargement of mainland species on islands) could be confirmed in their study of New Zealand birds. They argued that insular morphological evolution favours a large body size in bird species in habitats free of big mammals, like New Zealand. Body size enlargement is also favoured by the greater supply/demand of insular resources present in islands (Case 1978). Furthermore, the 'niche variation hypothesis' (Van Valen 1965) states these 'gigantic' insular birds have been found to experience niche diversification in the lack of potential predators and competitors, and performing ecological roles that they would not in other environments (Cassey & Blackburn 2004). Therefore, a large body size in islands seems to be a result of the combination of the decrease in predation pressure and interspecific competition (McNab 1971; Lomolino 1985) and dispersal needs (Adler & Levins 1994), as well as an increase in intraspecific competition (Robinson-Wolrath & Owens 2003). Conversely, shrinkage in large-bodied birds would not be strongly manifested in New Zealand because they would not have the need to dissipate heat as much as in low latitude islands (Clegg & Owens 2002; Cassey & Blackburn 2004).

McNab (2002) stated that instead of a strict 'rule', the insular body forms of vertebrates should be seen as dependent on the trade-off between usage and sharing of the insular availability resources, which is influenced by other ecological forces like the presence of predators. On one hand, most of the birds with herbivorous feeding habits on mainland would suffer a body size enlargement to occupy a niche that would normally correspond to browser and grazer large mammals. An increase in body size will also occur in species with feeding territories as a way to assure enough resource levels (Case 1978). On the other hand, species will experience a reduction in body size as a way to reduce the expenditure of energy and allow the preservation of larger populations (McNab 1994), but this decrease would not take place if other food resources are available or browser and grazer mammals are absent (McNab 2002) like in the islands of the ANZA region.

Apart from being free from predators and mammal species with browsing and grazing feeding habits which translates into vacant niches (Van Valen 1965; McNab 1971; Case 1978; Lomolino 1985; Cassey & Blackburn 2004), the islands of the ANZA region have some attributes that might have influenced the results of this research. The islands of the ANZA region have diverse origins based on tectonic plates movements and volcanism (Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009). Age, origin and other geological features, as well as biogeographic settings of islands, have proven to play an important effect on life-history traits and body size evolution of

reptiles (Novosolov & Meiri 2013) and mammals (Meiri et al. 2005b; Schillaci et al. 2009). Furthermore, as previously mentioned, birds would not express strong insular morphological shifts associated with thermoregulatory in the analysed islands due to their preponderance of high latitudes (Clegg & Owens 2002; Cassey & Blackburn 2004). Yom-Tov et al. (1999) maintained that the effects of insularity on body size of introduced rodents would decrease with higher latitudes because of a higher competition pressure on tropical islands than on temperate islands. Finally, the disproportion between the amount of small- and large-bodied birds in my data is consistent with the reality on temperate islands the ANZA region, where the majority of avian species are small because these islands were mostly colonized by these types of birds (Cassey & Blackburn 2004). Still, in their assessment on the presence of extreme bodied size species on islands, Meiri et al. (2011) found that the largest bird species within genera but not in other taxonomic levels were insular more often than expected by chance.

4.2 Insular sexual size dimorphism size

In the comparison between insular and mainland SSD, I did not find consistent evidence for greater divergence between species in insular species than in mainland species for any of the four traits. These results are consistent with the ones found by Van Valen (1965), who concluded that there were no greater size divergences between sexes in islands than in mainland. Considering that greater divergence between male and female morphology of insular bird species is mostly based on intraspecific competition (Selander 1966; Temeles et al. 2000), it can be presumed that this ecological factor was strong enough in the islands of the ANZA region as to boost its species enlargement but not a greater sexual morphological variance than in mainland. Just like in the evaluation of body size variations, the traits of the evaluated mainland-island bird species pairs could have not included the dramatic sizes of the traits for each species and maybe if more distantly in time and space related species were included the expected greater insular sexual size dimorphism pattern would have possible been expressed as in previous global studies (Clegg & Owens 2002; Lomolino 2005; Meiri et al. 2008).

4.3 Insular abiotic features as moderators of insular body size

I found diverse results when testing island area, distance from mainland and sea surface temperature as moderators of the mean effect sizes for wing, bill, tarsus and weight measurements. For the all combined and small-bodied species datasets, the AICc resulting values indicated that the best fitting models for each trait explained a substantial amount of the little SR variation and that they were clearly differentiated from the other models and the null model. The full model resulted as the best model for wing and weight measurements, while the sea surface temperature model fitted the best for bill lengths and the distance from mainland model fitted the best for tarsus lengths. As for the

large species dataset, the sea surface temperature model was clearly the best model for wing length. Conversely, for weight measurements of the all combined species dataset and for bill, tarsus and weight measurements of large species, the obtained AICc values for the tested models were not different enough from each other or from the null model as to certainly explain any variation in the SRs. Therefore, my findings suggested that island size and its distance from mainland did not explain insular body size variation as consistent as pointed out by most of the studies done in birds (e.g., passerines) (Clegg & Owens 2002; Lomolino 2005; Roulin & Salamin 2010).

As the SRs values were very similar to unity, there was little variation to be explained by the tested models. And, as the heterogeneity test values for the error (QE) were significant for all the fitted models, there was still a slight amount of heterogeneity that could not be accounted for in every tested model. Also, the multivariate models for weight measurements in the combined and large species datasets were fitted using the 'rma' functions, without accounting for the random effects because there were not enough replications. Most of the fitted models were good explanatory models of the small variation in SR. After selecting the best model for each trait, the three tested abiotic features were found to explain some of the slight SRs variations for all the combined. Weight measurements were negatively correlated with the distance from mainland and the sea surface temperature from this dataset. After the data was split according to their body length, these same results were obtained for small-bodied species. However, distance from mainland was positively but poorly correlated with weight measurements. The wing length of large-bodied birds had a negative correlation with the sea surface temperature. Then, island area, distance from mainland and sea surface temperature proved to be related to the SRs variations. But, considering that the SR values were highly similar to one, it is not clear if either of these abiotic features were important moderators of insular body size.

It has been assumed that different biotic and abiotic insular features affect morphological characters in birds with small and large body size differently (Grant 1968; Case 1978; Blondel 2000; Clegg & Owens 2002; Lomolino 2005). Nevertheless, independence between insular abiotic characteristics and relative insular body sizes was also found for carnivores (Meiri et al. 2005a; Meiri et al. 2006; Meiri et al. 2008; Raia et al. 2010a), reptiles (Meiri 2007) and amphibians (Wu et al. 2006). Heaney (1978), Lomolino (1985), and Adler and Levins (1994) claimed that the morphological shifts associated with the 'island rule' are manifestly stronger on more isolated islands. Considering that this study was restricted to the ANZA region, it is possible that the mainland-island regions were not distant enough to clearly reveal the expected patterns as observed by Meiri et al. (2008). More than three quarters of the analysed data came from islands that were located at less than 1000 km from the mainland. However, previous studies have found dramatic differences in body size in spatially close populations (Jessop et al. 2006).

Another explanation for the lack of concordance in the results of the tested moderators for small and large bird species could have been the difference between the used meta-analytic models. Meta-regression for weight measurements in the undivided data and large species data were fitted using the 'rma' functions, without accounting for the random effects because there were not enough replicates. This difference on the used meta-analytic models between small and large bird species for weight explains the dissimilarity on the resulting moderators for each group. Also, the disproportion between the amount of small and large species (the latter group had less than half pairs than the former for all the traits) is a possible explanation for the inconsistency between the moderators for the same traits in both the groups. Still, small-bodied birds are the majority of avian species worldwide (Blackburn & Gaston 1994).

On the other hand, several studies that criticize the generality, and even existence, of the 'island rule' recognize that the effects of insularity on the evolution of body size may be clade-specific, and contingency will have a relevant role in the distinct responses of each clade to distinct selective insular forces (Meiri et al. 2008; Meiri et al. 2011; Raia & Meiri 2011). I analysed my data at the family and order level as to explore these cladistics patterns, but found no consistent one. What is more, even though they are very distinct avian groups, I found no difference between the land birds and sea bird orders in their response to insularity. However, as shown in Figure 3.4, a large insular size increase was obtained when a couple of mainland (Australia) and insular (North Island, NZ) species from the Charadriiformes Order were compared. These results respond to a difference of 60 mm in wing length between NZ's *Charadrius obscurus* and Australia's *Charadrius ruficapillus*, as well as a difference of 16 mm between their bill lengths.

Sea birds have multiple morphological adaptations for specializing to marine life, like webbed feet and hydrodynamic wings (Marchant & Higgins 1990; Marchant & Higgins 1993; Greering et al. 2007; Gillespie & Clague 2009). Additionally, some studies have evaluated the effect of the presence of seabirds on the body size of insular vertebrates (Sanchez-Pinero & Polis 2000; Bonnet et al. 2002; Pafilis et al. 2011). Nevertheless, ocean-feeding birds are thought not to express insularity responses as strong as land birds because there is an uncertainty as to if their mainland and island forms have been exposed to different enough environments (Clegg & Owens 2002; Cassey & Blackburn 2004; Meiri et al. 2011).

Chapter 5

Conclusions and Recommendations

5.1 Conclusions

Overall, the estimated relative insular body size values showed small and inconsistent differences between mainland and insular closely-related bird species using wing, bill, tarsus and weight measurements as predictors of body size. Bill and tarsus followed a slight trend related to the 'island rule' pattern at the species level, but this trend did not remain present at the family or order level analyses. Also, the mean SR values of the four assessed traits suggest a weak trend for bird species to become larger on islands in spite of the body size of their mainland counterparts. Moreover, there were no consistent differences between the degrees of sexual size dimorphism in islands compared to mainland avian species. In addition, island area, distance from mainland and sea surface temperature showed a relation to SRs variations. However, because the estimated relative insular body size values were so close to one, it is not clear if either of these abiotic features were important moderators of insular body size. Subsequently, none of the proposed hypotheses for this research are supported. In conclusion, my findings do not provide enough support to validate the 'island rule' for the assessed birds of the ANZA.

5.2 Recommendations

During this research, I encountered some difficulties in the data compilation and analyses. I compiled the data trying to address some of the critics on past studies evaluating the 'island rule'. I worked with morphological information from sexed, adult avian specimens from single and not too large islands, and from the taxonomically and geographically closest mainland/island bird species pairs. One of the limitations in this study was the small amount of data within some families and orders, which did not allow the use of some statistical tests because of the lack of replications. This drawback was very relevant for the meta-analyses because I had to use a different type of model in one of these cases. Then, after dividing the data into small and large species, the former had more than twice the amount of data than the latter for all the traits. This imbalance could have also affected the expression of overall patterns. Another problem was the phylogenetic non-dependency of the data, which I tried to account for by including a random effect for family in the meta-analyses. Moreover, even though the analysed mainland/island pairs were established systematically like in past 'island rule' studies, my research was only focused on species within the ANZA region. So, it is possible that the analysed pairs were not chronologically and/or spatially separated enough as to show stronger, more consistent patterns like the ones found in past worldwide studies. Furthermore,

the assessed data was based on the HANZAB, which compiles many independent studies and sometimes did not include information about the season they took place on. I tried to overcome this source of bias by only collecting data from the studies where the season was indicated and matching them.

Considering these issues, I strongly believe that future studies assessing the 'island rule' should consider the next recommendations. Enough information should be collected for each taxonomic group to be able to perform the same type of statistical analyses on each clade at the family and order level. Equally proportioned amounts of data for small- and large-bodied size avian groups should be gathered. Moreover, the inclusion of some more direct indicators that reflect the biological attributes of different taxa and their insular ecological interactions like trophic level (e.g. predation or competition pressure) or territoriality might help understanding insular body size evolution of birds on a more deep level. Finally, future studies on avian evolution on islands should include phylogenetic comparative methods which were not used in this study because of the schedule and expertise in the subject. These methods will allow us to explicitly consider the absence of phylogenetic independence in the data and to recognize patterns within clades. The use of phylogenetic tools together with the inclusion of extinct species data could help reconstructing the evolution of birds' body size within islands could help improving the information to compare on each mainland/island pair for them to be more equally proportioned.

Appendix A

List of mainland species classified into small and large relative to their families mean body length (mm).

Order	Family	Family mean body length	mainland spp.	mainland spp. mean body length	size
Anseriformes	Anatidae	1050.0	<i>Anas castanea</i>	405.0	S
			<i>Anas platyrhynchos</i>	575.0	S
			<i>Anas superciliosa</i>	540.0	S
Caprimulgiformes	Aegothelidae	240.0	<i>Aegotheles cristatus cristatus</i>	230.0	S
	Podargidae	395.0	<i>Podargus strigoides strigoides</i>	435.0	L
Charadriiformes	Charadriidae	250.0	<i>Charadrius ruficapillus</i>	150.0	S
	Haematopodidae	455.0	<i>Haematopus longirostris</i>	495.0	L
	Laridae	495.0	<i>Anous stolidus</i>	415.0	S
			<i>Sterna bergii</i>	480.0	S
			<i>Sterna nereis</i>	245.0	S
	Recuvirostridae	430.0	<i>Himantopus himantopus</i>	375.0	S
Scolopacidae	390.0	<i>Calidris ferruginea</i>	205.0	S	
Columbiformes	Columbidae	450.0	<i>Ducula bicolor</i>	385.0	S
			<i>Phaps chalcoptera</i>	320.0	S
			<i>Phaps elegans</i>	290.0	S
Coraciiformes	Alcedinidae	160.0	<i>Alcedo azurea azurea</i>	180.0	L
			<i>Alcedo pulsilla ramsayi</i>	125.0	S
	Halcyonidae	280.0	<i>Todiramphus sanctus vagans</i>	220.0	S
Cuculiformes	Cuculidae	430.0	<i>Cacomantis flabelliformis</i>	260.0	S
			<i>Chrysococcyx lucidus plagosus</i>	170.0	S

			<i>Cuculus pallidus</i>	315.0	S
Falconiformes	Accipitridae	875.0	<i>Accipiter cirrhocephalus</i>	335.0	S
			<i>Accipiter fasciatus fasciatus</i>	475.0	S
			<i>Accipiter novaehollandiae</i>	465.0	S
			<i>Circus approximans</i>	555.0	S
	Falconidae	395.0	<i>Falco berigora</i>	460.0	L
Galliformes	Phasianidae	1320.0	<i>Coturnix ypsilophora australis</i>	195.0	S
Gruiformes	Rallidae	375.0	<i>Gallirallus australis australis</i>	480.0	L
			<i>Porphyrio porphyrio melanotus</i>	440.0	L
			<i>Tribonyx ventralis</i>	340.0	S
Passeriformes	Acanthisittidae	87.5	<i>Xenicus longipes longipes</i>	95.0	L
	Artamidae	320.0	<i>Artamus cyanopterus cyanopterus</i>	177.5	S
			<i>Artamus cyanopterus perthi</i>	177.5	S
			<i>Cracticus torquatus leucopterus</i>	285.0	S
			<i>Strepera versicolor versicolor</i>	505.0	L
	Callaeidae	365.0	<i>Philesturnus carunculatus rufusater</i>	250.0	S
	Campephagidae	255.0	<i>Coracina novaehollandiae melanops</i>	335.0	L
			<i>Coracina papuensis hypoleuca</i>	255.0	L
	Dicruridae	212.5	<i>Rhipidura fuliginosa alisteri</i>	152.5	S
	Maluridae	160.0	<i>Malurus cyaneus cyanochilamys</i>	175.0	L
			<i>Malurus leucopterus leuconotus</i>	122.5	S
			<i>Stipiturus malachurus parimeda</i>	172.5	L
			<i>Stipiturus malachurus polionotum</i>	172.5	L
			<i>Stipiturus malachurus westernensis</i>	172.5	L
	Meliphagidae	285.0	<i>Acanthorhynchus tenuirostris halmaturinus</i>	145.0	S
<i>Acanthorhynchus tenuirostris tenuirostris</i>			145.0	S	
<i>Anthochaera carunculata carunculata</i>			350.0	L	
<i>Anthochaera carunculata woodwardi</i>			350.0	L	
<i>Anthochaera chrysoptera chrysoptera</i>			310.0	L	

		<i>Anthornis melanura melanura</i>	185.0	S
		<i>Lichenostomus leucotis leucotis</i>	187.5	S
		<i>Manorina flavigula lutea</i>	250.0	S
		<i>Manorina melanocephala melanocephala</i>	260.0	S
		<i>Melithreptus lunatus lunatus</i>	130.0	S
		<i>Notiomystis cincta</i>	180.0	S
		<i>Phylidonyris novaehollandiae novaehollandiae</i>	180.0	S
		<i>Phylidonyris pyrrhoptera halmaturina</i>	155.0	S
		<i>Phylidonyris pyrrhoptera pyrrhoptera</i>	155.0	S
		<i>Prothemadera novaeseelandiae novaeseelandiae</i>	295.0	L
		<i>Ramsayornis fasciatus</i>	137.5	S
Motacillidae	172.5	<i>Anthus novaeseelandiae australis</i>	175.0	L
Muscicapidae	205.0	<i>Turdus merula merula</i>	250.0	L
		<i>Turdus philomelos clarkei</i>	220.0	L
		<i>Zoothera lunulata cuneata</i>	275.0	L
		<i>Zoothera lunulata lunulata</i>	275.0	L
Oriolidae	255.0	<i>Oriolus flavocinctus flavocinctus</i>	285.0	L
Pachycephalidae	190.0	<i>Colluricincla harmonica brunnea</i>	237.5	L
		<i>Mohoua albicilla</i>	150.0	S
		<i>Pachycephala olivacea bathychroa</i>	192.5	L
		<i>Pachycephala pectoralis youngi</i>	175.0	S
		<i>Pachycephala rufiventris falcata</i>	170.0	S
		<i>Pachycephala rufiventris rufiventris</i>	170.0	S
Pardalotidae	172.5	<i>Acanthiza chrysorrhoa leighi</i>	107.5	S
		<i>Acanthiza lineata clelandi</i>	100.0	S
		<i>Acanthiza pusilla pusilla</i>	102.5	S
		<i>Calamanthus campestris rubiginosus</i>	125.0	S
		<i>Calamanthus fuliginosus albiloris</i>	132.5	S
		<i>Gerygone igata</i>	100.0	S

			<i>Gerygone levigaster</i>	105.0	S
			<i>Pardalotus striatus substriatus</i>	105.0	S
			<i>Sericornis frontalis mellori</i>	127.5	S
	Passeridae	155.0	<i>Passer domesticus domesticus</i>	155.0	L
	Petroicidae	160.0	<i>Melanodryas cucullata picata</i>	162.5	L
			<i>Petroica australis australis</i>	180.0	L
			<i>Petroica macrocephala macrocephala</i>	130.0	S
			<i>Petroica multicolor campbelli</i>	125.0	S
			<i>Petroica phoenicea</i>	130.0	S
			<i>Petroica rodinogaster inexpectata</i>	122.5	S
	Sturnidae	285.0	<i>Acridotheres tristis tristis</i>	245.0	S
	Sylviidae	160.0	<i>Bowdleria punctata punctata</i>	120.0	S
	Zosteropidae	120.0	<i>Zosterops lateralis westernensis</i>	120.0	S
Pelecaniiformes	Phaethonidae	875.0	<i>Phaethon lepturus</i>	760.0	S
Podicipediformes	Podicipedidae	485.0	<i>Podiceps cristatus</i>	535.0	L
Procellariiformes	Hydrobatidae	195.0	<i>Oceanites oceanicus</i>	170.0	S
			<i>Oceanites oceanicus exasperatus</i>	170.0	S
	Pelecanoididae	215.0	<i>Pelecanoides urinatrix urinatrix</i>	225.0	L
	Procellariidae	620.0	<i>Halobaena caerulea</i>	290.0	S
			<i>Macronectes giganteus</i>	940.0	L
			<i>Pagodroma nivea</i>	350.0	S
Psittaciformes	Cacatuidae	475.0	<i>Calyptorhynchus funereus xanthanotus</i>	575.0	L
			<i>Calyptorhynchus lathamii lathamii</i>	480.0	L
	Psittacidae	540.0	<i>Cyanoramphus auriceps</i>	230.0	S
			<i>Glossopsitta concinna concinna</i>	220.0	S
			<i>Lathamus discolor</i>	250.0	S
			<i>Platycercus elegans elegans</i>	360.0	S
			<i>Platycercus eximius eximius</i>	300.0	S
Sphenisciformes	Spheniscidae	775.0	<i>Eudyptes pachyrhynchus</i>	630.0	S

			Eudyptula minor albosignata	425.0	S
			Megadyptes antipodes	710.0	S
Strigiformes	Strigidae	435.0	Ninox novaeseelandiae boobook	330.0	S
			Ninox novaeseelandiae novaeseelandiae	290.0	S
			Ninox novaeseelandiae ocellata	305.0	S
Struthioniiformes	Apterygidae	500.0	Apteryx australis mantelli	625.0	L

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