ECOLOGICAL CONSTRAINTS ON SOUTHERN HEMISPHERE AVIAN EVOLUTION.

by

Steven McGehee
BGs, Southeast Missouri State University, 1982

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

Supervisory Committee

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Abstract

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Much of Natural Science involves the study of patterns in nature and the documentation of how these patterns reflect and affect evolution. It is in this spirit that I have analyzed three distinct life history traits of austral South American forest passerines' to investigate whether their evolutionary patterns can be linked to evolutionary processes. This thesis reports six years of data on ten avian species from regular mist netting on Navarino Island, Chile. I found that the majority of species adhere to the same ecogeographical rules that govern the life history strategies of high latitude Northern Hemisphere birds. Eight of the species (Nancy says to list species but UVIC says abstract can only be a few words) have ancestors that originated in the tropics. The other two species have ancestors that originated in the Northern Hemisphere and expanded into the tropics where they evolved tropical life history strategies. The results of this study confirm the importance of the environment on avian speciation in newly accessible niches.

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> "*When on board H.M.S. 'Beagle', as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America... These facts seemed to me to throw some light on the origin of species-that mystery of mysteries, as it has been called by one of our greatest philosophers. On my return home, it occurred to me, in 1837, that something might perhaps be made out of this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it.*" Darwin 1850, (opening to *On the Origin of Species*).

In 1999, after many years of watching birds all over the world, I thought it necessary that I travel to Darwin's Patagonia and continue his "accumulating and reflecting on all sorts of facts" in order to throw more light on that "mystery of mysteries" the origin of species. I feel that I was amply rewarded for my efforts.

It was while I was mist netting on Navarino Island and wondering how best to write up the results, when Dr. Barry and Amanda Glickman sailed by on their sabbatical. It was their suggestion that my research could develop into a graduate degree, which led to this thesis. Dr. Glickman's advice, support and steady hand made this possible despite my best efforts to veer off course. My committee members Dr. Gregory, Dr. Stephenson and Dr. Turner gave many excellent suggestions, which greatly improved the thesis. Drs Ricardo Rozzi, Francesca Masasardo, Chris Elphick and Chris Anderson started the Omora Park bird research, without their continued support this study would not have been possible. Additional advice and assistance came from Ximena Arango, Edwardo Barros, Ivan Diaz, Ezio Firmani, Tomas Ibarra, Silvina Ippi, Herman Jose Gonzaléz, Jaime Jimenez, Ricardo Matus, Joan Morrison, Nicole Nemeth, Katie Sieving, Elke Schüttler, Juan Carlos Torres-Mura, Rodrigo Vásquez, Mary Willson, and many volunteers. Discussions with Don Allan, Brad Anholt, Michael Clinchy, Will Duguid,

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Dedication

"Felix qui potuit rerum cognoscere causas" Socrates
(Fortunate is the man who understands the causes of things)

To my parents Charles and Jennie McGehee who encouraged me through all these years to follow my dreams and now have something in their hands to show for it.

Chapter I

Introduction

One of the fundamental purposes of Biology is to study patterns in nature and to document how these patterns reflect evolution (Kingsland 1995). The field of Ecology has arisen partly to investigate these patterns. Yet many theoretical ecologists believe that what distinguishes Biology from all other sciences is absence of universal rules and facts (Roughgarden 1998). We need to ask why is the range of potential speciation probably restricted (Gould 1988) and are some of these restrictions caused by universal rules?

Because of their relative ease of study, their ability to quickly disperse into new areas and their apparent phenotypic plasticity, birds have served as model organisms in many fields of Biology (Ericson *et al.* 2006) and they have been a centerpiece of biological speciation theories (Ricklefs 2004, Grant and Grant 2008, Price 2008). Ernst Mayr, himself an ornithologist, used avian speciation in the South Pacific for the cornerstone of his landmark 20th century works on evolution (Haffer 2008).

To study avian speciation, one must focus on mechanisms of reproductive isolation in diverging populations. Both ecological and sexual selection may contribute to rapid morphological and behavioural divergence in allopatric species (Newton 2003). Species generally retain the ability to hybridize for millions of years after speciation, but nonetheless, often do not hybridize (Edwards *et al.* 2005). Johnson and Cicero (2004) compared calibrated molecular distance values of North American sister species and deduced that a substantial number of speciations occurred within the last 250,000 years. The current suggestion that speciation in birds generally takes around two million years is frequently an overestimate (but see Zink and Klinka 2006). The time requirement for avian speciation has been considerably shortened. Recently Wang *et al.* (2003) showed that North American House Finch (*Carpodacus mexicanus*) populations became genetically identifiable in as little as 50-100 years. Many evolutionary ecologists are coming to the conclusion that the real processes acting on speciation are not "...in the postzygotic genetics of interacting populations rebounding from allopatry, but in the prezygotic diversity of behavioural and ecological isolating factors, driven by changing environments in the great outdoors" (Edwards 2007).

Mila *et al.* (2006) showed that the Chipping Sparrow (*Spizella passerina*) migratory population descended from sedentary populations in Southern Mexico and they conclude that it was a northward expansion of the sedentary population after the last glacial maximum 18,000 years ago that led to the evolution of migratory behaviour. In this case both migration and the associated behaviours needed to genetically isolate a population appear to have evolved very rapidly or were possibly already present and only required an ecological change to reveal them.

Recent global ecological research has focused on identifying and understanding a group of patterns in nature known as ecological or evolutionary rules (Ashton, 2001). The defining of such rules has led to considerable discussion amongst ecologists who hold a range of opinions on the validity of these rules (Gaston *et al.* 1998, O'Hara 2006, Ashton 2001, de Queiroz and Ashton 2004, Hawkins *et al.* 2006, Meiri and Thomas 2007, Collin and Miglietta 2008, Diniz-Filho 2008). Regardless of this range of opinions, it is important to document and describe any general patterns in ecology and evolution because shared patterns can reveal common causality (Ashton 2001). Further, studying these patterns and their causes can help explain fundamental questions about biodiversity. For example, Kratina *et al.* (2007) have shown that the stability of an ecosystem depends greatly on its species diversity. The study of these rules offers the potential to infer how environmental conditions restrict the ability of organisms to persist and evolve (Nudds and Oswald 2007). Ultimately we can use these laws to build predictive theories (Turchin 2001).

The most widely studied ecological rule is one known as "Bergmann's Rule". Carl Bergmann (1847) reasoned that larger surface to volume ratios of a homeotherm would facilitate heat loss and a smaller ratio would aid in heat retention. He uncovered this fact by looking at similar sized animals and found that larger individuals did have a lower ratio of surface area to volume. He then deduced that smaller animals should, in general, inhabit warmer areas. From this he developed what became known as Bergmann's Rule, that there is an association between cold climates and body size. In most endotherm species Bergmann's rule has been found to be true. However, in ectotherm species, patterns appear more complex (Meiri and Thomas 2007).

Ernst Mayr called these rules "ecogeographical rules" and asked: "*What do the ecogeographical rules signify?-They are purely empirical generalizations describing parallelisms between morphological variation and physiogeographic features. For instance, Bergmann's rule states that "Races of warm blooded vertebrates from cooler climates tend to be larger than races of the same species from warmer climates." As Rensch has emphasized consistently, this is a purely empirical finding which can be proven or disproven no matter to what physiological theory one might ascribe this size trend. The validity of an ecological rule then does not depend on the validity of the physiological interpretation, but merely on the reliability of the empirical finding. To prove that an ecological rule is invalid one would have* *to prove that it is not valid in the majority of relevant cases"* (Mayr 1956, p. 105). These rules attempt to establish a relationship between a character gradient and some ecological gradient (Mayr 1956).

To test the validity of the mechanisms behind ecogeographical rules, ecologists need to collect data for multiple species and determine if a particular mechanism explains what is observed (Nudds and Oswald 2007). Recently de Queiroz and Ashton (2004) have shown that not only is one of the rules, in this case Bergmann's, valid for Tetrapods, but that it appears to show species-level heritability because this trait's origin predates the evolution of endothermy. This suggestion is that the tendency to adhere to Bergmann's rule may be an ancient trait shared by numerous taxa. Yom Tov *et al.* (2006) explored the question of body size and temperature by examining their relationship in Great Britain. They found that over the last thirty years as temperatures have increased the body size of 14 species of British passerines has decreased. It is surprising that although Bergman's rule has been demonstrated to hold for the majority of endotherm species (Meiri and Thomas 2007), only two South American species are included in that list (*Diglossa carbonaria and Amblycercus holosericeus*) (Graves 1991, Kratter 1993). Ashton (2001) has proposed that before investigating the processes responsible for these patterns, ecologists should first document that these patterns are indeed universal. South America has many allopatric and sympatric avian species deserving study regarding this evolutionary question. Recent studies have looked at South American avian species to explore the processes that drive avian species richness (Vuilleumier 1991, Rahbeck and Graves 2001), clutch size (Yom-Tov *et al.* 1994), and Rapoport's Rule in Andean passerines (Ruggiero and Lawton 1998). Analyzing my data from Navarino Island in Southern Chile will help reveal the degree to which the evolutionary forces that shaped speciation in the Northern Hemisphere have done the same in the Southern Hemisphere.

Documentation of life history traits of Southern Hemisphere passerines will lead to the development of a hypothesis for the differences and/or similarities in evolution between two hemispheres' temperate forest songbirds (Jahn *et al.* 2002). This research took place on Navarino Island, Chile (54°) (Appendix b: Figure 1). In this study I chose to investigate whether avian life history traits of species inhabiting ecosystems at high latitudes have formed through similar evolutionary processes driven by ecogeographical patterns.

In Chapter II, I evaluate whether Bergmann's Rule applies to the birds of the high latitudes of South America. Recent studies have found Bergmann's rule to hold for the majority of birds, mammals, fish and insects studied in the Northern Hemisphere (Ashton 2001), but it is unknown whether this rule is exhibited in South American birds. Documenting and understanding the mechanisms that underlie consistent patterns in body size in nature would contribute substantially towards the goal of making theorem driven predictions in evolution possible.

Chapter III describes the monthly fluctuations of body mass of six Southern Chilean passerines. Northern Hemisphere passerines fatten during periods of high metabolic demand. Parallel trends of mass fluctuation between Southern Hemisphere and Northern Hemisphere birds would indicate similar ecological adaptations to similar climates, glacial history and habitat.

The first part of Chapter IV describes the study of moult in nine avian species from Southern South America and investigates the use of moult limits to determine the age of

South American birds. In order to understand age-related differences in reproductive success, survivorship, habitat selection etc., easy and accurate methods for determining the age of a bird in the hand are needed. European and North American breeding and migrating birds are routinely aged and sexed based on moult patterns. Books are available that describe the majority of Northern Hemisphere species (Jenni and Winkler 1994, Pyle 1997), but a recent survey by Pyle (2006) revealed that only 8% of the neotropical landbird species have had their moult and age determination characterized. Specifically, we know next to nothing about moult in Austral South American passerines. Population demographics and habitat usage studies in the Neotropics have been hampered by the lack of sexing and aging criteria (Ryder and Durães 2005). I investigate the results from the capture and banding of 6702 birds of 21 different species on Navarino Island supplemented with information obtained from bird skins in museums in Chile. Data from the examination of the moult in known, aged birds allow me to determine the moult limits in six species of birds belonging to four families of passerines. This will assist South American ornithologists in the more accurate aging of birds in the field as well as those in museum collections.

The second part of Chapter IV also explores moult in Austral South American species. Moult is an essential component in the annual cycle of birds because worn feathers detrimentally affect survival, thermoregulation, waterproofing, courtship display, dermal parasite infestation and flight. Birds use moult to replace worn feathers or in some cases to change plumage. Temperate zone birds live in an environment that changes throughout the year. Moulting in Northern Hemisphere birds has been well studied and shown to be an activity that requires much energy along with being absolutely essential for survival. Nothing is known of the moult in the Austral species of South America (Bairlein 2001). Do the same ecological forces acting on Northern and Southern Hemisphere (i.e. similar temperatures) birds produce the same moulting strategies even though they are not phylogenetically related?

I propose the following hypothesis for this study: *That avian species in the same latitudes in North and South America will show similarities in life history strategies even though they have been geographically separated for many millions of years.* Genetic drift, mutation, gene flow, etc. should all have contributed to differences such as those seen between life history traits of Northern Hemisphere and tropical bird species. . I predict that avian species from similar taxa in North America, Europe and Southern South America are shaped by the same ecological rules and follow similar speciation patterns.

My research provides insights into whether the same ecological processes that shaped avian evolution in the Northern Hemisphere are also operating in the Southern Hemisphere. Higher latitudes appear to have a faster transition time to speciation for birds (Weir and Schluter 2007). Yet if environmental factors only allow certain genotypes to survive this should be reflected in those species that colonize newly opened habitats. The data presented here indicate that ecogeographic rules are likely one of the major forces driving the process of speciation because they occur in parallel in both hemispheres.

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Chapter II

AUSTRAL SOUTH AMERICAN PASSERINES AND BERGMANN'S RULE: DOES IT HOLD?

Abstract

Birds, like other animals, exhibit a range of body sizes both within and between similar species. Such variation is not random; there appear to be patterns in the evolution of body size. The most widely studied ecogeographical rule on body size variation is Bergmann's rule which states that organisms tend to be larger at higher latitudes, i.e., cooler climates. This is thought to be an adaptation to heat loss as reduced surface area to volume ratio in larger organisms improves heat conservation. Recent observations have reconfirmed the validity of Bergmann's rule across several taxa including mammals, bird, turtles, salamanders, etc. Whether passerines in the Southern Hemisphere also obey this rule has not been confirmed. In this study therefore, I mist netted 2330 birds of ten species inhabiting the higher latitudes of Southern Chile and compared their mean mass to the same ten species from studies 1520-3300 km further north in Central Chile and Argentina. I found that eight of the ten species adhere to the rule. This is the first time that Bergmann's Rule has been confirmed for the Southern Hemisphere. Remarkably, these eight species descend from tropical lineages where Bergmann's rule is not followed, indicating that our observations also demonstrate the evolutionary change in body weight with latitude.

Keywords: Bergmann's rule, body size, birds, passerines, Chile, evolution, Southern Hemisphere

Introduction

For much of the last 150 years evolutionary biologists have been trying to identify large-scale patterns in nature (MacArthur 1972). One such pattern is the predictable fluctuation of body size within particular environmental parameters (Ashton 2001). Patterns in evolution of body size are of particular interest as body size affects many life-history traits of an organism (Rodríguez *et al.* 2006, Stillwell *et al.* 2007) making body size variation the likely product of natural selection (Maurer 2003).

In 1847 the German biologist, Carl Bergmann, proposed that warm-blooded animals at warmer latitudes would be smaller than their counterparts at higher or cooler latitudes (Bergmann 1847). This rule, which has become known as Bergmann's Rule, thus describes the relationship between morphological variation and ambient temperature and has been shown to be generally valid for changes of body weight with latitude (Meiri and Dayan 2003). Blackburn *et al.* (1999) suggested that Bergmann's rule should be reformulated as "the tendency for a positive association between the body mass of a species . . . and the latitude", rather than between body size and temperature. This definition has at least two advantages over Bergmann's original definition. First it frames Bergmann's rule in terms of body mass rather than any other parameters that may change with latitude (such as wing length as predicted by Allen's rule), and second, it relates body mass variation to variation in latitude rather than to climate.

The responsible evolutionary driver of Bergmann's Rule remains the subject of discussion. At least seven different theories had been proposed to account for its validity. These range from the classical heat retention theory, to larger body size conferring greater resistance to starvation (Jones *et al.* 2005). If it is temperature that drives Bergmann's rule, then the effects of even a modest change in global climate could be enormous (Yom-Tov *et al.* 2008). In light of the current predictions about how quickly temperatures may rise, the implications are potentially very serious (Millien *et al.* 2006). The body size of a number of birds and mammals has already been shown to be decreasing in response to higher temperatures in Europe (Millien *et al.* 2006).

In their review of the literature, Millien *et al.* (2006) found Bergmann's Rule to apply to between 62% and 83% of all vertebrate species. A recent review of Bergmann's rule in birds (Ashton 2002a) found it to be generally valid for birds in the Northern Hemisphere. He also discussed several theories that have been proffered to account for the underlying mechanism but conclude that more work is required before we can expect to understand the process that drives this ecogeographical rule. It has also been pointed out that the mechanism responsible for the pattern described by Bergmann's rule may not be the same as the mechanism that maintains it (Losos 1992). An oft-quoted example is the development of feathers, which may have first evolved as a means of thermoregulation and only later have been refined to permit flight (Rayner 1991).

The similarities in the life history traits of North American and European birds have been repeatedly noted. For example, clutch size increases with increasing latitude in the Northern Hemisphere in both the Old and the New World (Yom-Tov *et al.* 1991). This has also been shown for birds in Southern Africa (Moreau 1944) and similar trends, though less dramatic have been observed in Eastern Australia (Yom-Tov 1987). However, based on a study of estimated clutch sizes from general field guides, Yom-Tov *et al.* (1994) concluded that in South America, clutch sizes did not increase at higher latitudes. It has recently been found that tropical bird species, especially in South America, have lower testosterone levels than temperate species during the breeding season (Garamszegi *et al.* 2008). Further Northern Hemisphere-Southern Hemisphere differences include avian migrational patterns. Migrational patterns are similar in North America and Europe and unknown in North Asia, whereas in South America these patterns are much more complex and do not operate in a single direction, e.g., north-south (Jahn *et al.* 2006).

South America supports almost one-third of all living bird species (Graves and Rahbek 2005). Because of its temporal isolation, South America, like Australia and Madagascar, has been considered a hotspot for the evolution of new avian phenotypes (Price 2008). In addition, in South America 93% of the species are endemic. This is the highest level of endemism of any continent (Newton 2003), which may reflect the isolated evolutionary history of the South American landmass (Newton 2003, Price 2008). As recently as 14,000 years ago, much of the southern portion of the continent was covered in glaciers (Villigrán 1988), and the impact of glaciations on South America's avian history remains largely unknown (Vuilleumier 1991). Determining whether ecological patterns hold for species colonizing recently unglaciated areas should provide interesting insights into the mechanism underlying Bergmann's rule.

In studies of Bergmann's rule in South American birds, both the Carbonated Flowerpiercer (*Diglossa carbonaria*) and Yellow-Billed Cacique (*Amblycercus holosericeus*) body size was highly correlated with latitude (Graves 1991; Krater 1993). However, four other tropical species did not show adherence to Bergmann's rule. These include the Sepia-brown Wren (*Cinnycerthia peruana*), the Light-crowned Spinetail (*Cranioleuca albiceps)* (Brumfield and Remsen 1996), the Marcapata Spinetail (*Cranioleuca marcapatae)* (Remsen

1984) and the White-throated Spadebill (*Platyrinchus mystaceus*) (Remsen *et al.* 1991). None of these studies directly considered the relationship between latitude and temperature, although as the species considered are all located quite close to the equator, variation in temperature may be insufficient to affect body size. In other words, South America remains largely unknown ecologically making it fertile ground for comparison of the evolution of ecogeographical rules within and between clades (Jahn *et al.* 2006).

In this study, I have used body mass of wild caught birds to assess the validity of Bergmann's Rule in Southern South America avian species. I hypothesize that, because Southern South America has greater extremes of temperature than tropical South America, the species inhabiting high latitudes of South America are more likely to show latitudinal patterns in body size. Finding evidence of rules in this geographically isolated region will go a long way to support my hypothesis that Bergmann's Rule occurs in both hemispheres. .

Methods

The study site is Navarino Island located just south of the island of Tierra del Fuego, Chile (Figure 1). In a general survey of avian populations initiated in 1999, birds in the Omora Ethnobotanical Park (54°57'S 67°39'W) have been mist netted in a systematic manner at sites ranging from 5 to 500 meters above sea level. Two sites in Omora Park, approximately 420 meters apart, were used each month. Both sites were operated for three days each month for a total of six days in the park. These sites have been surveyed every month from January 1999 until April 2006. Three to six mist nets were opened every day from one to four hours after sunrise. The nets were checked every 15 minutes and left open for 5 to 11 hours each day. During high winds (>24KH), snow, rain or low temperatures

(<2°C) the nets were closed. Opportunistic mist netting was also performed at a number of sites on the north end of Navarino Island, all within 500 meters of the Beagle Channel.

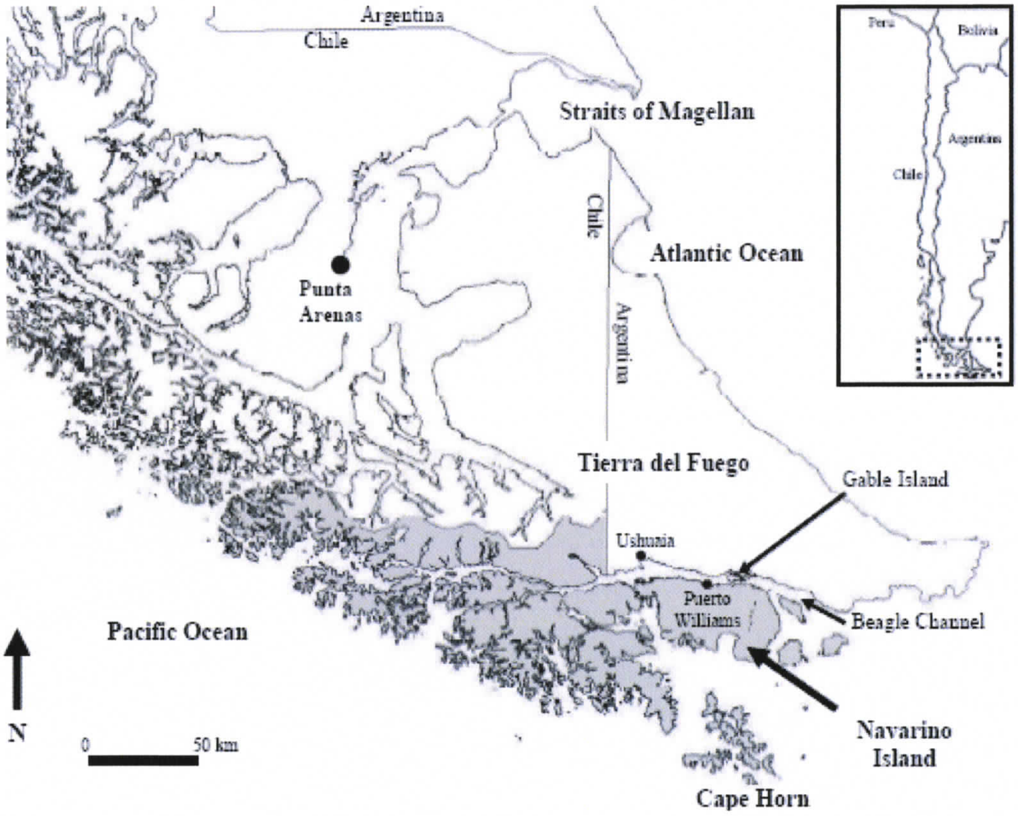

Figure 1. Map of southern South America, showing the Cape Horn Biosphere Reserve (in grey). Study sites were located on Navarino Island (54-55°S), Chile.

Figure 1: Study site Navarino Island, Chile (From Ibarra *et al.* 2009)

All birds captured were identified according to Araya *et al.* (1996) and Couve and Vidal (2003) and by comparison with skins in El Instituto de Patagonia, Punta Arenas and El Museo de Historia Natural, Santiago. The capture, banding, and handling of birds were authorized by Servicio Agrıcola y Ganadero of Chile. Captured birds were aged (McGehee *et al.* 2006) and sexed using known diagnostic characteristics, presence of brood patch, or left unsexed and unaged. Birds were removed from nets as quickly following capture as possible, placed into bags and mass (Chardine 1986) was obtained using 10, 60, 100 or 500-gram Pesola™ scales. Body mass was measured to within 0.1g or, for the 100 and 500 gram scales, to 0.5 grams. All birds were banded with aluminum bands containing a unique number combination to prevent pseudoreplication (Anderson *et al.* 2002).

Body mass, which takes into account an organism's nutrient reserves and structural framework, is a measure of the overall size of an organism (Dunning 2008). Body mass varies throughout the year and between sexes (Winker 1998). Body mass is frequently used as a surrogate for body size when analyzing Bergmann's rule (Katti and Price 2003, Ramirez *et al.* 2007, Teplitsky *et al.* 2008). Wing length also is often used as the measurement for body size (Ashton 2002a), but these additional measurements were generally missing from most other Chilean and Argentinean bird studies. The bird body masses from most other studies used for comparison were not separated by sex. Therefore in this study body mass was an average of both sexes.

Techniques for sexing and aging South American temperate passerines are still under development (McGehee *et al.* in prep). It has been shown that some species of birds exhibit nonlatitudinal intraspecific spatial variation in body size, which means using a single average mass for a species may either over-or under-estimate true body size of a population (Ashton 2002). The data was collected throughout the year, although the majority were captured from October to March. Bird weights from lower latitude studies that were used here for comparison were either collected throughout the year, or only during the summer months. Most reports of bird mass unfortunately do not list when the data were collected so current studies still use mean mass from any time of the year when more temporally collected data are unavailable (Ramirez *et al.* 2007, Greve *et al.* 2008).

All of my data and those from other studies involved birds captured at an altitude of 500 meters or less, which helps limit any possible effect of elevation on bird mass (Ramirez *et al.* 2007). Recaptures account for less than 1% of all captures, but birds were included in the data if the recapture was in a later year. I also measured wing cord and tail length of all birds captured. I used principal components analysis on the wing length, tail length and mass of each adult non-moulting bird caught to determine if I could obtain a better estimate of body size than just mass alone (Guillaumet *et al.* 2008).

Data were collected for ten species: White-crested Elaenia (*Elaenia albiceps chilensis*), Tufted Tit-tyrant (*Anairetes parulus lippus*), and Fire-eyed Diucon (*Xolmis pyrope pyrope*) (Tyrannidae); Thorn-tailed Rayadito (*Aphrastura spinicauda spinicauda*) (Furnariidae); Chilean Swallow (*Tachycineta meyeni*) (Hirundinidae); House Wren (*Troglodytes aedon chilensis*) (Troglodytidae); Austral Thrush (*Turdus falcklandii magellanicus*) (Turdidae); Black-chinned Siskin (*Carduelis barbata*) (Fringillidae); Rufous-collared Sparrow (*Zonotrichia capensis australis*) (Emberizidae); and Patagonian Sierra-finch (*Phrygilus patagonicus*) (Thraupidae) (Table 1). Associated weather data came from Schwerdtfeger (1976), except for Central Chile (Tapia 2005), Llao Laao Argentina (Amico and Aizen 2005) Chiloe Island, Chile (Figueroa and Castro 2002) and Navarino Island (Pisano 1977) (Table 1).

For comparisons with birds on Navarino Island, we used mass data from Contraras (1975), Foster (1987), Egli (1996), Amico and Aizen (2005), Ippi *et al.* (2005), Moreno *et al.*

(2005) and Dunning (2008). We used a two-sample *t* test (Zar 1999) to test whether there is a difference in mean mass between populations at different latitudes. We make the assumption that all samples come from normally distributed populations and have equal variances. Because the data from lower latitudes comes from papers that list only the mean mass and the standard deviation or standard error, we used standard formulae to calculate *t* (Zar 1999). An analysis of variance was performed between latitude and mean annual temperature and mean yearly precipitation. A principle components analysis along with the Kaiser-Meyer-Olkin measure of sampling adequacy and a Bartlett's test of sphericity was performed on each species using mass, wing length and tail length. The Kaiser-Meyer-Olkin measure of sampling adequacy investigates if the partial correlations among the variables are small. A KMO number should be above 0.5 to contunue with a factor analysis. Bartlett's test of sphericity investigates the appropriateness of using a factor model (Newcastle University 2007). Data were analyzed with SPSS 11.0.0.

Results

Eight of the ten bird species sampled adhere to Bergmann's rule (Table 2; Figure 2). The two species that did not follow Bergmann's rule are the migrant White-crested Elaenia and the year-round resident Austral Thrush ($p<0.05$). A principal components analysis of wing length, tail length and mass showed that seven species (Tufted-Tit Tyrant, House Wren, White-crested Elaenia, Fire-eyed Duicon, Thorn-tailed Rayadito, Chilean Swallow and Black-chinned Siskin) did not meet the Kaiser-Meyer-Olkin Measure of Sampling Adequacy ($p<.6$) nor Bartlett's Test of Sphericity ($p>.05$) (Table 3). Therefore the correlations in the data set for these species were not appropriate for factor analysis and we used only mass for assessing Bergmann's rule (Bruin 2006). An analysis of variance between latitude, total yearly precipitation and mean yearly temperature, showed a significant relationship between temperature and latitude (p<.007), but not between latitude and precipitation (p<.425).

Table 1: Species, location, sample size, mass, yearly precipitation and mean annual temperature for each species observed in this study.

Species	**Location**	Mass in grams (SD, range: min-max)	**Lat**	**Long**	**Yearly precipitation (mm)**	**Mean Annual Temperature (C)**	**Source**
Rufous-collared Sparrow	Navarino Is. Chile	23.1 (1.32,19.9-26.0)	54°57'S	67°39'W	467	6.0	TS
Rufous-collared Sparrow	Central Chile	21.5 (1.5, 18.0-26.4)	33°29'S	70 °54'W	356	14.0	1
Rufous-collared Sparrow	El Tirol, Paraguay	20.1 (4.25, NA)	27 11'S	55 47'W	1695	21.1	2
Tufted Tit-tyrant	Navarino Is. Chile	6.9 (0. 38, 6.0-7.5)	54°57'S	67°39'W	467	6.0	TS
Tufted Tit-tyrant	Central Chile	6.2 (0.5, 6.3-7.5)	33°29'S	70 °54'W	356	14.0	1
Chilean Swallow	Navarino Is. Chile	16.3 (1.18, 13.6-19.1)	54°57'S	67°39'W	467.3	6.0	TS
Chilean Swallow	Central Chile	14.9 (0.6, 14.0-16.0)	33°29'S	70 °54'W	356.3	14.0	1
Black-chinned Siskin	Navarino Is. Chile	16.5 (1.12, 13.5-19.9)	54°57'S	67°39'W	467	6.0	TS
Black-chinned Siskin	Central Argentina	15.5 (1.4, 13.0-19.8)	41°08'S	71°26'W	717	8.3	3
Fire-eyed Diucon	Navarino Is. Chile	41.8 (2.71, 36.6-45.5)	54°57'S	67°39'W	467	6.0	TS
Fire-eyed Diucon	Central Argentina	35.3 (3.2, 31.0-42.4)	41°08'S	71°26'W	717	8.3	3
Patagonian Sierra-finch	Navarino Is. Chile	23.2 (1.44, 19.1-27.5)	54°57'S	67°39'W	467	6.0	TS
Patagonian Sierra-finch	Central Argentina	22.6 (1.9, 19.1-27.4)	41°08'S	71°26'W	717	8.3	3
House Wren	Navarino Is. Chile	10.6 (0.71, 9.3-12.8)	54°57'S	67°39"W	467	6.0	TS
House Wren	Chiloe Is. Chile	10.0 (0.5,NA)	41°52'S	73 39'W	2200	9.5	4
House Wren	Central Chile	10.4 (0.9,NA)	33°29'S	70 °54'W	356	14.0	1
White-crested Elaenia	Navarino Is. Chile	16.1 (1.15, 13.7-20)	54°57'S	67°39'W	467	6.0	TS
White-crested Elaenia	Central Chile	16.5 (2.21, 12.5-23.7)	33°29'S	70 °54'W	356	14.0	1
White-crested Elaenia	Chiloe Is. Chile	16.6 (1.18, 14.0-21.0)	41°52'S	73 °39'W	2200	9.5	5
White-crested Elaenia	Central Argentina	15.5 (1, 13.4-17.8)	41°08'S	71°26'W	717	8.3	3
White-crested Elaenia	Llao Llao, Argentina	15.8 (22.1,NA)	41°00'S	71°30'W	1800	9.0	6
Thorn-tailed Rayadito	Navarino Is. Chile	12.5 (1.14, 10.1-15)	54°57'S	67°39'W	467	6.0	TS
Thorn-tailed Rayadito	Chiloe Is. Chile	11.3 (0.51, NA)	41°52'S	73 39'W	2200	9.5	7
Austral Thrush	Navarino Is. Chile	91.6 (3.69, 84.5-99.7)	54°57'S	67°39'W	467	6.0	TS
Austral Thrush	Llao Llao, Argentina	88 (19.12, NA)	41°00'S	71° 30'W	1800	9.0	6

Source: TS; present study, 1: Egli (1996), 2: Foster (1987), 3: Contreras (1975), 4: Ippi *et al.* (2005), 5: Espinosa and Egli (1997), 6: Amico and Aizen (2005), 7: Moreno *et al.* (2005).

Table 2: Table of t and p values of two-tailed t test between mass means of different populations of birds in this study along with location and distance between study sites.
X=lower latitude birds have higher mean weight than the higher latitude birds they are compared to.

Species	Location	Distance in kilometres between sites	t + p
Rufous-collared Sparrow	Navarino Is. Chile vs Central Chile	2,390	11.63 p<0.05
Rufous-collared Sparrow	Navarino Is. Chile vs El Tirol, Paraguay	3,300	6.849 p<0.05
Tufted Tit-tyrant	Navarino Is. Chile vs Central Chile	2,390	7.11 p<0.05
Chilean Swallow	Navarino Is. Chile vs Central Chile	2,390	5.227 p<0.05
Black-chinned Siskin	Navarino Is. Chile vs Central Argentina	1550	8.412 p<0.05
Fire-eyed Diucon	Navarino Is. Chile vs Central Argentina	1550	6.507 p<0.05
Patagonian Sierra-finch	Navarino Is. Chile vs Central Argentina	1550	2.198 p<0.05
House Wren	Navarino Is. Chile vs Chiloe Is. Chile	1520	3.939 p<0.05
House Wren	Navarino Is. Chile vs Central Chile	2,390	2.1623 p<0.05
White-crested Elaenia	Navarino Is. Chile vs Central Chile	2,390	X
White-crested Elaenia	Navarino Is. Chile vs Chiloe Is. Chile	1520	X
White-crested Elaenia	Navarino Is. Chile vs Central Argentina	1550	5.12 p<0.05
White-crested Elaenia	Navarino Is. Chile vs Llao Llao, Argentina	1550	.32746 p>0.05
Thorne-tailed Rayadito	Navarino Is. Chile vs Chiloe Is. Chile	1520	11.1 p<0.05
Austral Thrush	Navarino Is. Chile vs Llao Llao, Argentina	1550	.8541 p>0.05

Table 3: Principal components analysis of mass, wing length and tail length for each species in this study.

Species	**KMO Score**	**Bartletts p value**	**df**	**Sample size**
Patagonian Sierra-finch	.603	.000	3	550
House Wren	.455	.009	3	110
Rufous-collared Sparrow	.571	.000	3	58
White-crested Elaenia	.499	.000	3	256
Chilean Swallow	.464	.501	3	35
Thorn-tailed Rayadito	.518	.089	3	53
Tufted Tit-tyrant	.599	.276	3	21
Black-chinned Siskin	.497	.134	3	183
Fire-eyed Diucon	.501	.068	3	14

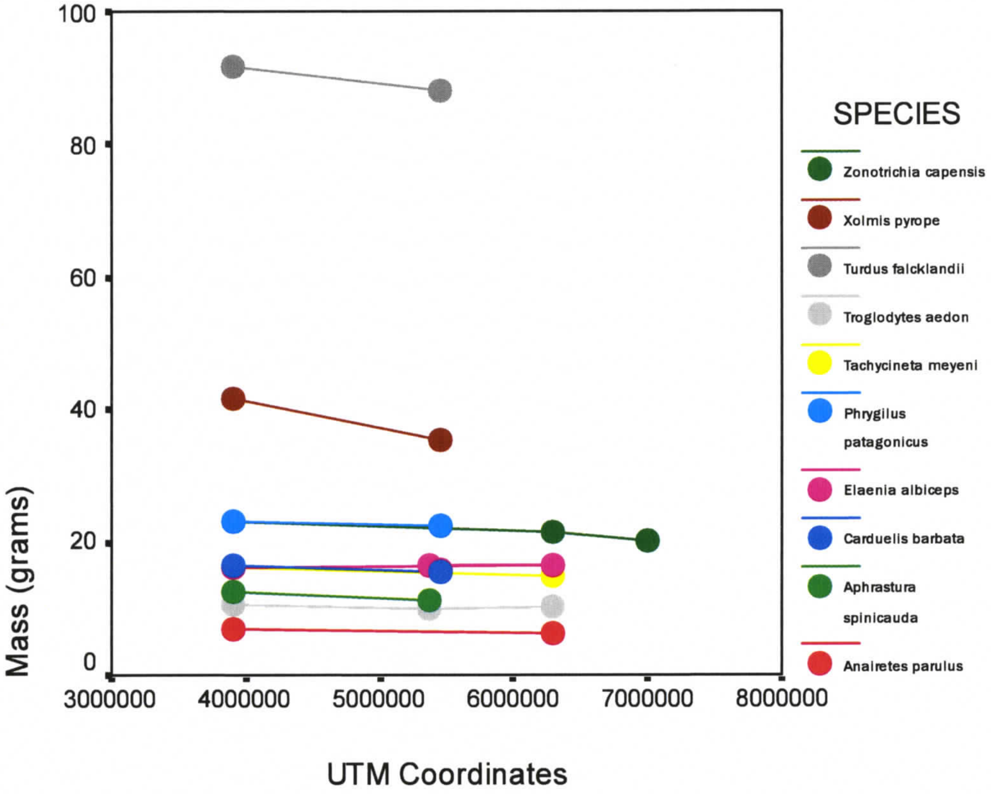

Figure 2: Graph of mass vs latitude for the ten species in this study. Mass (grams) is the mean of the mass for each location. Latitude is in the Universal Transverse Mercator Coordinate System.

Discussion

In order to access the validity of ecogeographical rules, empirical data from multiple species is gathered and then compared. Bergmann's rule equates geographical distribution to morphological variation (Nudds and Oswald 2007). Eight of the ten species of birds examined in this study showed increased body mass with increasing latitude. Two species did not obey Bergmann's Rule; they are discussed below.

The White-crested Elaenia is a long distance migrant and therefore its lack of adherence to Bergmann's rule is not surprising. This species leaves Southern South America in the autumn (February-March) and spends its winters (April-August) in Brazil and Paraguay (Fjeldså and Krabbe 1990). In the Northern Hemisphere, species that migrate long distances are much less likely to have a latitudinal cline in body size (Ashton 2002a, Meiri and Dayan 2003). It is thought that because migrants leave to escape the harsh winter they are consequently unaffected by Bergmann's rule which is less relevant (Meiri and Dayan 2003). Interestingly, the other long distance migrant in our study, the Chilean Swallow does, however, adhere to Bergmann's Rule. A similar observation has been made for some North American and European migrant passerines (Ashton 2002a), possibly reflecting either an historical past or the characteristics of the migration pattern. In the case of the Chilean Swallow no details are available as to where it spends the winter (Fjeldså and Krabbe 1990).

The Austral Thrush is a member of a worldwide genus and is one of the heaviest of that family (Dunning 2008). Normally larger birds are found to comply with Bergmann's rule and indeed the Northern Hemisphere thrushes that have been studied do adhere to Bergmann's rule. This makes our result somewhat unexpected as other *Turdus* adhere to Bergmann's rule (Ashton 2002a). However, we do take our results with a degree of caution considering the small sample size of only 24 individuals, combined with quite high standard deviations. A larger dataset is required to finalize conclusions on the Austral Thrush.

This studies approach suffers from some limitations. Ideally all mass data should be collected on a single date. Secondly, as male and female birds have different weights, mixing of the data from the two sexes can increase the variance. Consequently where Bergmann's rule is not confirmed, this may reflex technical limitations and the possibility exists that this reflects the studies technical limitations. However, these limitations have not impeded the ability to undertake this study. Bergman's rule is here demonstrated as the majority of species analyzed adhere to the rule. It is also noteworthy that most studies on Bergmann's Rule, even recent ones, are subjected to the same limitations (Ramirez *et al.* 2007, Greve *et al*. 2008, Treplitsky *et al*. 2008).

In North and South America a strong temperature effect on body size among phylogenetically related avian species has been reported (Ramirez *et al.* 2007). For Isla Navarino regional weather data are limited to precipitation and temperature. As seen in other studies (Ashton 2002a), we also found a significant relationship between temperature and latitude, but not precipitation. There is as yet insufficient data to provide a completely satisfying universal explanation for the process responsible for Bergmann's rule (Blanckenhorn *et al.* 2006). The mechanism behind Bergmann's rule may be complex and may involve more than one factor, as is the case with other ecogeographical rules (Lomolino 2005). Our addition of new examples from the previously unexamined southern part of a southern continent contributes more pieces to the puzzle and helps to confirm the global validity of this rule.

Greve *et al.* (2008) found that Bergmann's rule did not hold for most of the bird species (900+) in Southern Africa. However, their study suggests that environmental variables, particularly South Africa's mild winters, may account for the minimal variation in bird body mass. The winters in Southern South America (5.2° C average) are considerably colder than those in Southern Africa, which average about 10° C. Though in the low lands of Southern Chile freezing occurred only very rarely during the day. It seems likely then that the Southern South African winter temperatures are above the critical point that triggers

Bergmann's Rule (Rodríquez *et al.* 2006). Bergmann's rule does not need to be found in every species to be valid. This study shows that Bergmann's rule is, however, valid over a much larger area of the Earth than previously thought (Ashton 2002a). When different species across the same land mass show the similar variation in the same phenotype (ie mass) this emphasizes the role of natural selection on local adaptations (Newton 2003).

There is a range of opinion as to whether inferences can be made regarding Bergmann's rule from intra versus interspecific comparisons. Diniz-Filho *et al.* (2008) emphasized the importance of evaluating ecogeographical rules at intraspecific levels. . Remsen (1982) gave a paper dismissing Bergmann's rule for Andean birds. Ramirez et al. (2007) concluded that South American birds adhere to Bergmann's rule, but made only an interspecific analysis based upon data in bird field guides and did not look at differences within species. The confirmation of Bergmann's rule in South America offers some unique insights into the evolutionary processes at work and the time required for such forces to be phenotypically expressed. Considering that the retreat of the glaciers that once covered the region was completed only about 14,000 years ago (Villagrán 1988), and these recent colonizers have a tropical origin, the change appears to have been very rapid. Recent work indicates that avian evolution rates can be extremely high (Hairston *et al.* 2005).

The past few years have seen a plethora of papers reinforcing the validity of a number of ecogeographical rules that had mostly been discarded by ecologists (Ashton 2001, 2002a,b, Clegg and Owens 2002, Jones *et al.* 2005, Hone and Benton 2007, Meiri *et al.* 2007, Nudds and Oswald 2007, Miller *et al.* 2008). Whatever the actual mechanism, it is clear that when the environment reaches a critical level of harshness, rules such as Bergmann's rule quickly come into play. McNamara *et al.* (2008) have presented a model demonstrating that if all else is equal, in an avian species, a seasonal environment produces an avian life history of a typical temperate avian species. Eight of ten species in this study increased in mass with increasing latitude. This provides partial support for the hypothesis. This study adds to the growing body of literature validating an ecogeographical rule.

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Chapter III

SEASONAL BODY MASS CHANGES IN SIX FOREST PASSERINES OF SOUTHERN CHILE

Abstract

I investigated fluctuations of monthly body mass of six Southern Chilean passerines including: the migrant White-crested Elaenia (*Elaenia albiceps*); the House Wren (*Troglodytes aedon*); the Rufous-collared Sparrow (*Zonotrichia capensis*); and the year-round residents Thorn-tailed Rayadito (*Aphrastura spinicauda*); the Patagonian Sierra-Finch (*Phrygilus patagonicus*); and the Black-chinned Siskin (*Carduelis barbata*). The migrant species each demonstrate a mass peaking just prior to the autumn migration. The Southern Chilean resident species all showed a general decrease in mass during the winter months. This is in contrast to many Northern Hemisphere passerines that tend to fatten during periods of high metabolic demand such as winter. I interpret these observations as an indication that the mild winters of Southern South America are not as energetically demanding as winters at similar latitudes in the Northern Hemisphere.

Key words: *mass, birds, Southern Chile*

Introduction

Body mass of birds has been used extensively as an indicator of general condition in life history studies of birds (Moreno 1989), as well as a measure of body size as a baseline descriptive statistic when species are being compared (Dunning 2008). Considerable data has been collected on the monthly body mass fluctuations of both Northern Hemisphere migrant and resident birds (Rands *et al.* 2006). It has been found that body mass of Northern Hemisphere birds varies daily and seasonally because of changes in their body fat content and their reproductive condition (Baldwin and Kendeigh 1938; Clark 1979; Rands *et al.* 2006). Northern Hemisphere birds generally will accumulate body fat reserves before seasonal events that have high-energy demands or low food availability. Examples of such events include incubation periods, migration and harsh winter conditions (Koenig *et al.* 2005). Northern latitude long-distance migrants experience the greatest change in body mass, which can be a gain of up to 100% of their pre-migration mass (Clark 1979). Many resident species show an increase in body mass during autumn that peaks midwinter. This fluctuation has been labelled the "winter fattening strategy" (Baldwin and Kendeigh 1938, Haftorn 1989) and is generally associated with ground-foraging birds (Cooper 2007). The body mass of tree-foraging birds appears much less likely to vary seasonally, probably reflecting their more predictable food supply (Cooper 2007).

Migratory fattening is controlled by an innate program of circannual response which is thought to be predominantly synchronized by changes of photoperiod (Gwinner 1986; Berthold 1996; Haftorn 1989; Rintamäki *et al.* 2003), while winter fattening shows high plasticity and may be under the control of environmental factors such as temperature and/or food predictability (Biebach 1996; Totzke *et al.* 2000). Lindsdale and Sumner (1934a, 1934b) found that the Golden-crowned Sparrow (*Zonotrichia coronata*) on its California wintering grounds not only gained mass in winter, but also reached an even greater peak just before its spring migration. In a study of individually marked birds, Haftorn (1989) found that most individuals of five European Tit (*Parus*) species followed the classic winter fattening strategy in which body mass increased during autumn to a midwinter peak around December, after which it declined. Koenig *et al.* (2005) found that significant winter fattening occurs in some non-migratory woodpecker species. The differences in ecology between species in the Northern Hemisphere has an effect on how the cost of events like migration, reproduction and food availability are manifested, but the trend of mass gain to counter the cost of physically taxing events is generally noticeable (Koenig *et al.* 2005).

One of the most impressive adaptations to Northern Hemisphere migration is the deposition of migratory fat prior to migration (Berthold *et al.* 2003). But few studies have been done on Southern Hemisphere birds to observe if this adaptation also exists in those species (Martin 1996). One study in Australia discovered that the Yellow-faced Honeyeater (*Lichenostomus chrysops*) does not show pre-migratory fattening in autumn. However, this species does commence spring migration with ample fat reserves. Large masses and fat reserves have also been found in other Australian passerines, including Eastern Spinebills (*Acanthorhynchus tenuirostris*) and New Holland honeyeaters (*Phylidonyris novaehollandiae*). These high masses probably reflect the greater energy demands during periods of low temperature (Berthold *et al.* 2003). According to the adaptive winter-fattening hypothesis (Lehikoinen 1987), body mass of resident birds should increase gradually in autumn reaching a maximum in midwinter and then decrease towards spring. Fat reserve increases and mass gains are thought to be an adaptive response of birds to unpredictable food supplies and foraging times in winter (Rintamäki *et al.* 2003).

In this study I analyze seasonal body mass fluctuations of migrant and resident passerine species in Southern Chile to ascertain if their fattening strategies parallel Northern Hemisphere birds.

Methods

The study was carried out on Navarino Island in Southern Chile. Mist netting was conducted primarily at two sites on the northern coast of the island: the Omora Ethnobotanical Park (54°57'S; 67°39'W), near the town of Puerto Williams, and on Guerrico Hill (54°55'S; 67°54'W) 17 kilometres to the west (Anderson and Rozzi 2000). Both sites are relatively low elevation, ranging from sea level to 100 m. Additional mist netting, accounting for less than 1% of the dataset, was conducted at several other places on the island, including some with an elevation as high as 250m. The Omora Ethnobotanical Park comprises a mosaic of diverse forest types, which include old growth forests dominated by *Nothofagus* species, as well as naturally and anthropogenically perturbed forests and the disturbance effects of the introduced beaver (*Castor canadensis*) since the 1960s (Anderson *et al.* 2006). Among the latter is a shrub land area dominated by the shrub Firebush (*Embothrium coccineum*), adjacent to evergreen forests of Coigüe (*Nothofagus betuloides)* on a north-facing slope of Robalo Mountain. The other site on Navarino Island is a north-facing slope on Guerrico Hill. This slope has been logged and is now dominated by the shrubs *E. coccineum* and Mata negra (*Chillotrichium diffusum*). This area is 30 meters from a forest of *Nothofagus betuloides* and *N. pumilio*, adjacent to the main dirt road along the Northern coast of Navarino Island.

Navarino Island is characterized as an oceanic climate type with a mean annual temperature of 5.6°C and an annual temperature fluctuation of less than l0°C. Moreover, minimum temperatures below 0°C occur only during the winter months of July and August, and temperatures below -5°C are rare. In 2000, minimum mean monthly temperature was 1.6°C and maximum mean monthly temperature was 10.2 °C. The average annual rainfall in Puerto Williams is less than 500 mm (Anderson *et al.* 2002).

Starting in 2000, mist netting was conducted on a monthly basis on Navarino Island (Anderson and Rozzi 2000). The nets were open 6 days each month in Omora Park from January 2000 to May 2006. The nets were checked every 15 to 40 minutes depending on weather and number of birds caught. Birds were also mist netted near Guerrico River up to 15 days each year. All birds captured were placed in a bag and taken approximately 30 meters away from the nets where they were then rapidly processed. They were identified to species and sexed and aged where possible. Their mass was then measured with a Pesola™ spring balance accurate to 0.1 grams (Moreno 1989, Gosler 2004), while remaining in the bag, with the weight of the bag subtracted.

For this study I used the weights of the following resident forest species: Thorn-tailed Rayadito *(Aphrastura spinicauda),* Patagonian Sierra-Finch (*Phrygilus patagonicus)*, and the Black-chinned Siskin (*Carduelis barbata)* and the migrant species White-crested Elaenia *(Elaenia albiceps*), House Wren *(Troglodytes aedon*) and Rufous-collared Sparrow *(Zonotrichia capensis*). The elaenia, rayadito and wren are primarily tree and aerial foragers. The sierra-finch and siskin are primarily tree foragers but will forage on the ground. The sparrow is a ground forager. Data from January 2000 to November 2001 were previously reported in Anderson *et al.* (2002).

Dunning (2008) indicates that for ecological and physiological studies, when a baseline body size is necessary for descriptive statistics, adult body mass is the best single estimator of avian body size. For this reason, juvenile body masses were not included in the study. The total body mass of an individual is the most convenient standard for energetic comparisons, but mass can be a deceptive measure of body size because of variation within individuals and within species due to metabolic costs (Clark 1979).

In a broad analysis of mass measurement techniques, Rands *et al.* (2006) showed that mass has been recorded in many different ways and some techniques can produce an observer effect on the mass of the birds. For example, rapid mass loss can occur following a stressful event such as mist netting (Rands and Cuthill 2001), even in the moments between capture and weighing. Therefore all mist netted individuals were treated identically in order to minimize this potentially confounding component. The complication of pseudoreplication (Hurlbert 1984) was avoided as all birds captured in this study were banded with uniquely numbered aluminum bands. For those birds that were subsequently recaptured only the first weight was used unless it was not taken during the first capture.

I define the reproductive season as the period October through February, post-reproductive season from March through May, and pre-reproductive season from June through September (McGehee, unpublished data, Table 4). Furthermore, migrants are defined as species that leave the area in the post-reproductive season and return at the end of the pre-reproductive season (Newton 2008). This study did not take into account the natural fluctuations of resources between years and the effect this can have on the overall annual fluctuation of bird mass. If during one winter resources were scarce, while during another winter bountiful, this would likely be reflected in the observed masses of the birds (Rands *et al.* 2006). Also because our sample sizes for most species are small, I used masses taken at all hours of the day (Dunning 2008) (Figure 3). Spearman Rank Correlations were performed on the data to see if there was a correlation between mass and time of day measured (Moreno 1989).

All data were pooled across years to increase sample size. One-way ANOVA tests were performed to see if there was a difference in weights between months. A factorial ANOVA was performed to see if a significant pattern of change across months was different among years. TukeyHSD tests were run between monthly groups in each species to uncover for which months there was a statistical difference in mass mean (Zar 1999). All analyses were carried out using the statistical package R, Version 2.4.1 (R Development Core Team 2005).

Results

There were variations in mass between some months (Table 5). TukeyHSD tests showed that a significant difference ($p<0.05$) was found between some monthly mass averages within each species (Table 6). For 3 species, Black-chinned Siskin, House Wren and Thorn-tailed Rayadito, there was not a significant difference between mass and time of capture (Table 7). Results of the factorial ANOVA (Table 5) showed that for two species there was a significant difference between the same months in different years.

The migrant birds showed an increase in mass prior to autumn migration. The White-crested Elaenia (Figures 4,5,6) increased its body mass prior to autumn migration and then returned from its wintering grounds with an even larger mass, which decreased as eggs were laid and chicks were reared. Elaenia migrated with their lowest mass during their time on the breeding grounds. The House Wren (Figures 4,5,6) returned from migration with its lightest mass, which then began to increase in the period leading into reproduction. It then increased its mass with its highest mass occurring during fledging period and just before migration. The Rufous-collard Sparrow (Figures 4,5,6) showed an increase in mass during the reproductive period but then a decrease in mass in the month of February at the start of autumn migration.

Resident birds showed a more consistent mass across the year, with some significant decreases in the winter months. The Thorn-tailed Rayadito (Figures 4,5,6) had an almost constant mass year round with the only significant differences in mass between two winter months and February when fledges were still being fed The Black-skinned Siskin (Figures 4,5,6) also only had a significant difference in mass between midwinter (July) and the months of the reproductive season. The Patagonian Sierra-finch (Figures 4,5,6) had a mostly uniform mass all year around. Its lightest mass was in September before the start of the reproductive season with a slight increase until the end of the reproductive season.

Table 4. Distribution of months by seasons, and the Southern Chilean passerine annual lifecycle of reproduction and migration. sum=summer, aut=autumn, win=winter, spr=spring, repo=reproduction, mig=migration.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
sum	sum	aut	aut	aut	win	win	win	spr	spr	spr	sum
repo	repo	mig	mig	mig	mig	mig	mig	mig	mig	repo	repo

Table 5: Results of two-way ANOVA with month nested in year for all six species in this study.

Species	n	p year	df	p month	df	p month*year	df
Thorn-tailed Rayadito	432	.544	5	.067	11	.743	22
White-crested Elaenia	251	.726	3	.000	3	.661	4
House Wren	159	.255	5	.000	4	.619	10
Rufous-collared Sparrow	146	.492	3	.000	5	.582	9
Patagonian Sierra-finch	759	.506	5	.000	11	.062	21
Black-chinned Siskin	232	.597	4	.109	6	.400	8

Table 6: Post hoc TukeyHSD test of months with a list of months where there is a significant (p<0.05) different in mean mass.

Species	Months	p	Species	**Months**	p
Thorn-tailed Rayadito	July-December	.014	Patagonian Sierra-finch	July-February	.001
Thorn-tailed Rayadito	July-February	.002	Patagonian Sierra-finch	August-February	.007
Thorn-tailed Rayadito	February-April	.010	Patagonian Sierra-finch	Sept.-November	.000
Thorn-tailed Rayadito	February-May	.000	Patagonian Sierra-finch	Sept.-December	.000
Thorn-tailed Rayadito	May-December	.001	Patagonian Sierra-finch	September-February	.000
White-crested Elaenia	November-January	.001	Patagonian Sierra-finch	September-March	.000
White-crested Elaenia	November-February	.002	Patagonian Sierra-finch	September-May	.001
White-crested Elaenia	December-January	.001	Patagonian Sierra-finch	September-June	.000
White-crested Elaenia	December-February	.005	Patagonian Sierra-finch	October-February	.000
House Wren	October-January	.000	Patagonian Sierra-finch	October-April	.000
House Wren	November-December	.000	Patagonian Sierra-finch	October-June	.046
House Wren	November-January	.000	Patagonian Sierra-finch	November-February	.001
House Wren	November-February	.002	Patagonian Sierra-finch	December-February	.000
House Wren	December-January	.001	Patagonian Sierra-finch	December-April	.045
Black-chinned Siskin	July-December	.000	Patagonian Sierra-finch	January-February	.000
Black-chinned Siskin	July-January	.003	Patagonian Sierra-finch	January-April	.004
Black-chinned Siskin	July-February	.025	Patagonian Sierra-finch	February-March	.000
Black-chinned Siskin	July-May	.000	Patagonian Sierra-finch	February-April	.031
Black-chinned Siskin	July-June	.010	Patagonian Sierra-finch	February-May	.000
Rufous-collared Sparrow	September-October	.004	Patagonian Sierra-finch	April-May	.004
Rufous-collared Sparrow	September-November	.004			
Rufous-collared Sparrow	September-December	.000			
Rufous-collared Sparrow	September-January	.000			
Rufous-collared Sparrow	October-January	.004			
Rufous-collared Sparrow	November-January	.041			
Rufous-collared Sparrow	January-February	.002			

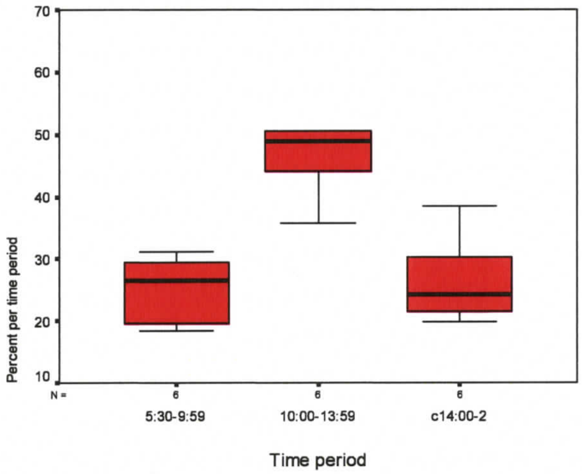


Figure 3: Box Plot of percentage of birds caught in each time period (with 95% confidence levels, first and third quartiles) during mist netting in this study with. All six species are combined

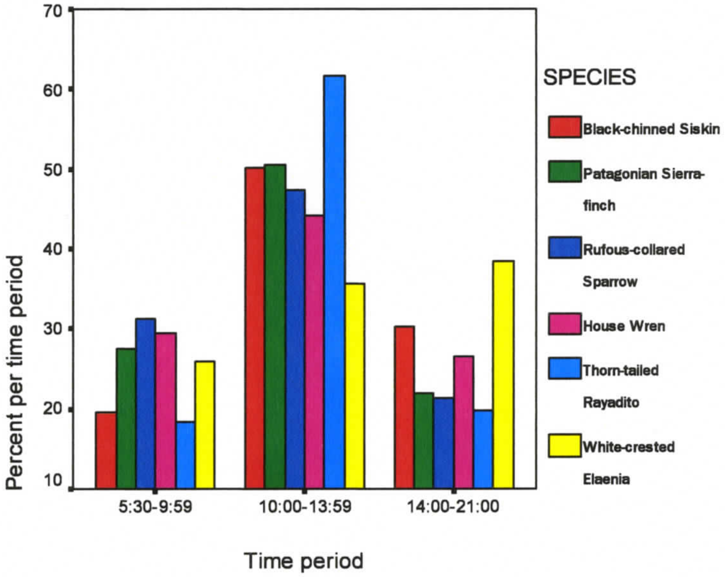
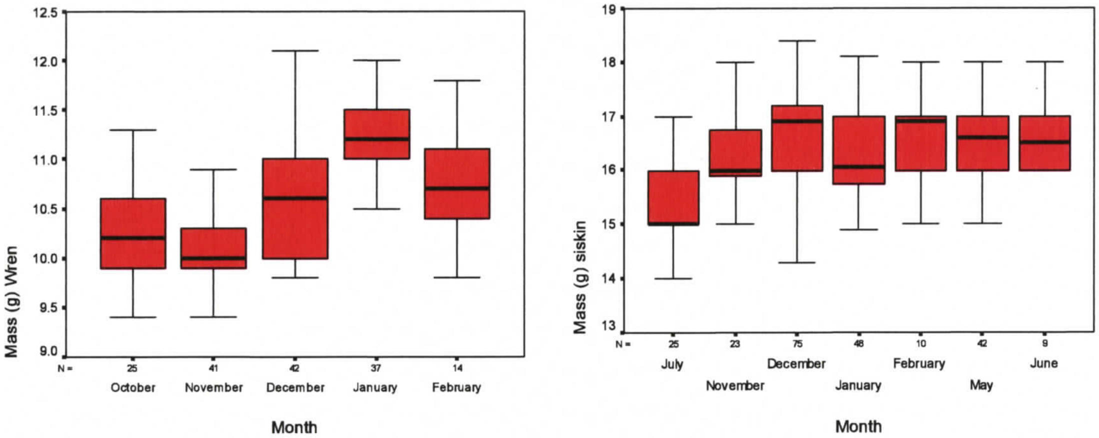
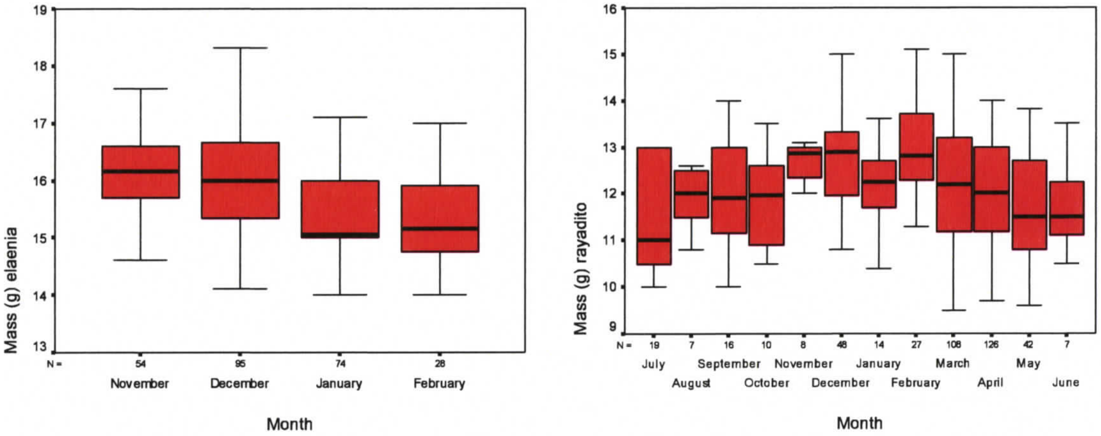


Figure 4: Graph of time periods each species was caught during mist netting .



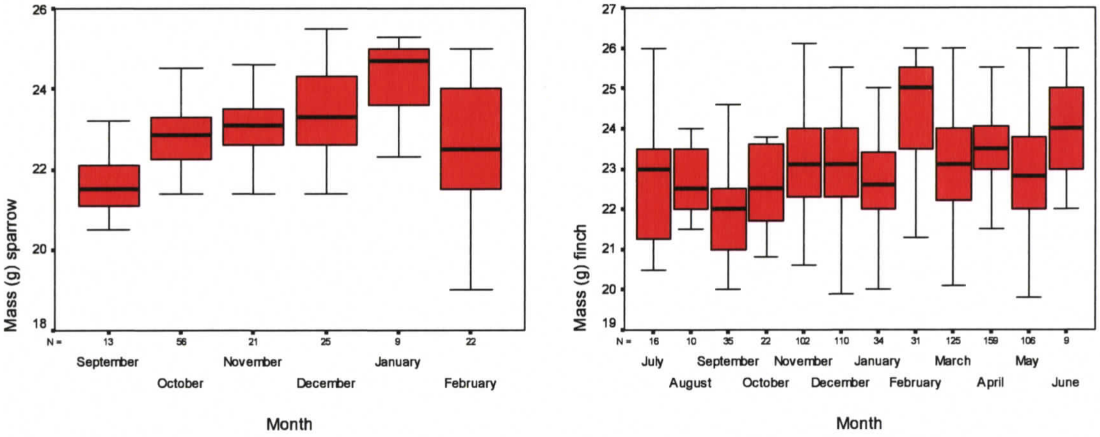
House Wren

Black-chinned Siskin



White-crested Elaenia

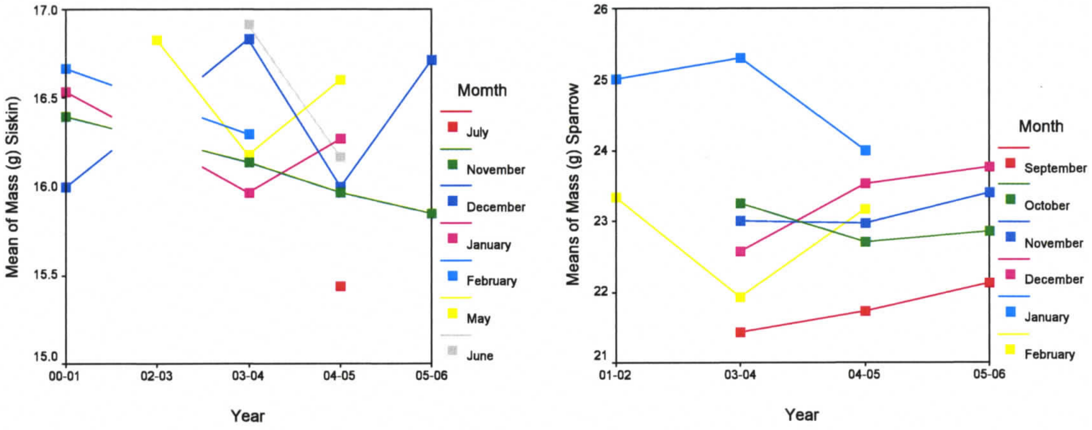
Thorn-tailed Rayadito



Rufous-collared Sparrow

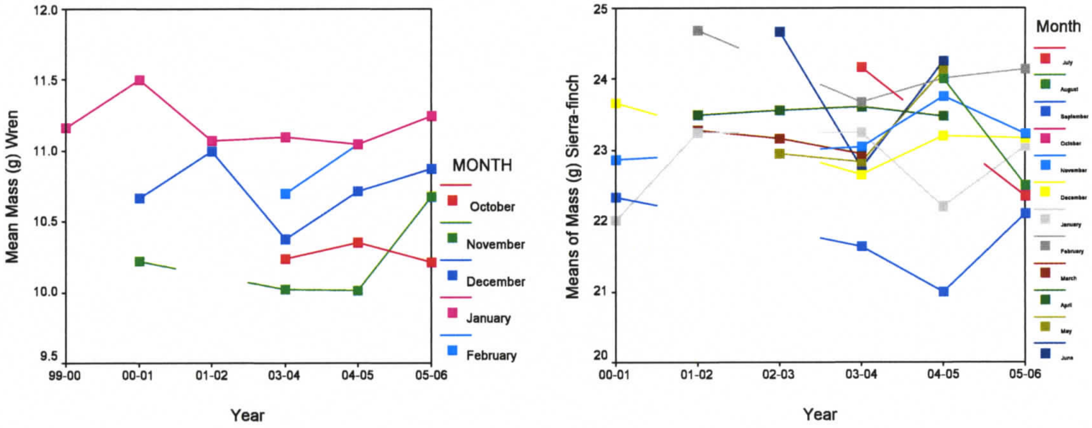
Patagonian Sierra-finch

Figure 5: Monthly mass average (with 95% confidence levels) for each species of birds in this study with first and third quartiles. All years were combined.



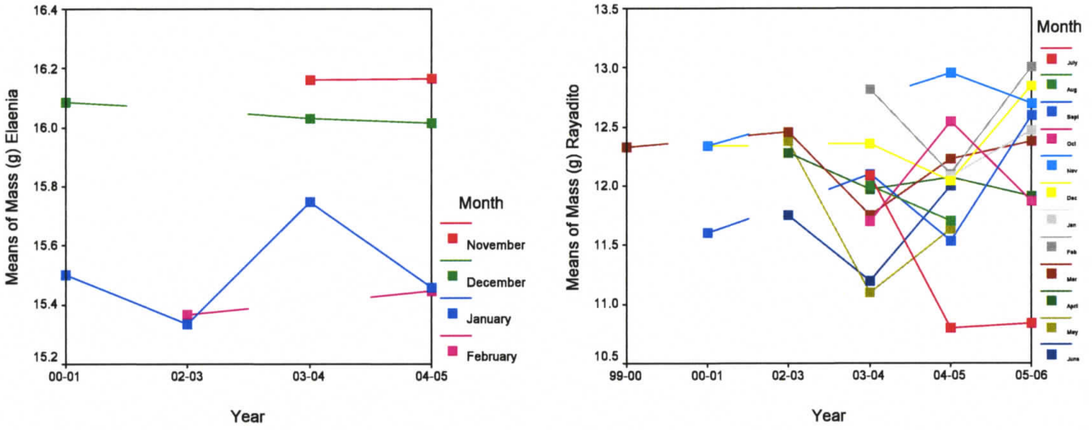
Black-chinned Siskin

Rufous-collared Sparrow



House Wren

Patagonian Sierra-finch



White-crested Elaenia

Thorn-tailed Rayadito

Figure 6: Graphs of mean bird weights per month for each year

Table 7: Spearman Rank Correlations between mass and time of day

Species	p
Thorn-tailed Rayadito	.060
White-crested Elaenia	.000
House Wren	.704
Rufous-collared Sparrow	.005
Patagonian Sierra-finch	.000
Black-chinned Siskin	.898

Discussion

In our study we found that two of the three migratory species showed seasonal mass patterns similar to their Northern Hemisphere counterparts. White-crested Elaenia showed a general trend of decreasing mass in the two months leading up to autumn migration (Figures 4,5,6). This could be due to increased competition for food from recently fledged Elaenias or the cost to adults of feeding fledglings. According to Marini and Cavalcanti (1990), the White-crested Elaenia has two migration routes, one along the eastern slope of the Chilean Andes and the other from Argentina towards the Atlantic coast and up to the Brazilian Amazon. These migratory routes provide this species with the potential to feed on its way back to the reproductive grounds in Chile and there is some evidence that Elaenias do feed during migration (Hiriart *et al.* 2000). It is possible that higher masses at the end of migration are a result of food consumed during migration or an abundance of food on their wintering grounds (Schaub and Jenni 2000, Newton 2004). There was no loss of body mass when the birds arrived on their breeding ground as is common in Northern Hemisphere birds, indicating a sufficient amount of food is available in early summer (Biermann and Sealy 1985)

The partial migrant House Wren had its highest average annual mass in January and its lowest average mass in October and November (Figures 4,5,6). Though nothing is known about the migratory routes or wintering grounds of this wren (del Hoyo *et al.* 2005), its post-migration low mass is consistent with the ecology of Northern Hemisphere House Wrens (*Troglodytes*), which exhibit low mass after migration and a slow gain after the chicks fledge (Taylor *et al.* 1983, Biermann and Sealy 1985). A few individuals of this species are seen on Navarino during the winter months (McGehee and Arango unpublished data). This species gained mass after its return from migration, unlike Northern Hemisphere migrants, also indicating there is sufficient food at the start of the reproductive season.

The partial migrant Rufous-collared Sparrow shows little significant mass difference throughout the year, although a general trend towards increased mass is observed prior to autumn migration. Its lowest annual mass is recorded in September (Figures 4,5,6). Like the other two migrants it too has a drop in mass just before it migrates. This could be that those birds remaining in February do not leave until they have gained sufficient weight. It appears that the Southern Chilean populations are partially migratory, but it may be that some of their winter destinations are not more than 200 kilometres away (McGehee unpublished data, Chapman 1940, Couve and Vidal 2003), thus reducing the metabolic costs of migration to the bird and minimizing mass fluctuation over the year.

The resident species we studied showed a different yearly weight regime from Northern Hemisphere residents. The Thorn-tailed Rayadito did not show an overall significant difference in mass between all months (p>.067). There were, however, some differences between individual months (Figures 4,5,6). The Rayadito showed little or no winter fattening, with its mid-winter mass being its annually lowest mass. The foraging strategy of the Rayadito is opportunistic. It mainly eats insects in the warm months of the year (Moreno *et al.* 2005), while in the fall and winter months it has been documented to consume seeds and fruits (Estades 2001, del Hoyo *et al.* 2003, McGehee 2007). Its opportunistic nature may decrease the effect that low winter food resources generally have on Northern Hemisphere birds leading to a stable mass during the winter season.

The resident Black-chinned Siskins also have smaller average masses in midwinter, though their mass appears to remain constant up to the onset of winter in May and then drops in July (Figures 4,5,6). Mass in July is significantly lower than in December. Their diet and foraging strategies are still relatively unknown (Achuby *et al.* 2007). A lack of sufficient birds captured precluded a full 12-month analysis of siskins.

The resident Patagonian Sierra-finch has its lowest mass in September (Figures 4,5,6). Generally its mass appears to fluctuate little over the year, but there is a general trend of increase from September to February, followed by a decrease back to September. This could be explained by the rather varied diet of the Sierra-finch on Navarino Island (McGehee and Eitniear 2007) decreasing the need for a seasonal fattening strategy.

All three year-round residents showed constant mass or a drop in mass during the winter and not an increase, as seen in most Northern Hemisphere species. The adaptive winter-fattening hypothesis states that fat and therefore body mass should increase during the winter when food supplies are most unpredictable (Lehikoinen 1987). Rintamäka *et al.*

(2003) studied two species of tits (*Parus*) and found that it was a decrease in photoperiod and less so a decrease in temperature that caused winter fatting. Species in our study area are at 4 degrees lower in latitude than the *Parus* sps. in the above study. Navarino Island has a much milder winter than similar latitudes in the Northern Hemisphere. The average temperature in the winter on the island is 2ºC (Tuhkanen *et al.* 1989). Therefore it is not surprising that winter fatting was less pronounced in Southern Chile. No birds in this study were seen to cache food for the winter (McGehee, unpublished data), which would negate the need for putting on winter fat (Cooper 2007).

The surprise results of this study are that Southern Chilean forest passerines show little statistically significant changes in mass throughout the year, unlike high latitude Northern Hemisphere passerines. The three largest species (Sierra Finch, Siskin and Sparrow) along with the smaller Rayadito maintained their mass during the breeding season unlike in Northern Hemisphere birds (Biermann and Sealy 1985), implying that there isabundant food resources during this period and the larger birds do not need to adapt the strategy of lowering their mass to decrease energy used during this highly energetically demanding period.

The body mass strategies of Southern Hemisphere passerines appear to differ from their Northern Hemisphere relatives. In this study, it was found that three resident species of Southern Chilean passerines failed to show any trend towards winter fattening, with the average mass of the Thorn-tailed Rayadito and the Black-chinned Siskin being at their annual lowest in midwinter. Conversely, in Northern Hemisphere species, winter fattening is a very common strategy for coping with resource limitation (Biebach 1996). Adaptive pre-migratory fattening was observed in two Southern Chilean species; this strategy is shared with many Northern Hemisphere relatives. Such different trends of mass fluctuation in Southern Hemisphere birds, compared to trends in Northern Hemisphere birds, reflect the different environment of those species (Biermann and Sealy 1985, Berthold *et al.* 2003). Other recent research has shown these six species have similar life history strategies as those species inhabiting ecologically similar latitudes in the Northern Hemisphere (McGehee in prep). The results of this study confirm that the local environment can play an important role in determining life history strategies (Martin and Tewksbury 2008). The question that these results lead to is: if winter is so mild in the high latitudes of South America that resident species do not need to put on winter fat, then why have not more species colonized this area and why do any migrate out? Previous to this study there was very little data with which to infer the similarities or differences between Northern and Southern temperate Hemisphere bird life histories. Much of what we think we know may be incorrect or overstated (Martin 1996). Southern Hemisphere birds represent a particularly interesting system for studying the evolution of life history strategies. Rigorous documentation of demographic life history traits will substantially advance knowledge, and such information will lead to the development of hypotheses for the differences and similarities in those processes that influence life history evolution between Northern versus Southern Hemisphere species and temperate vs. tropical species (Martin 1996, Newton 2003).

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Chapter IV

AVIAN MOULT AND MOULT LIMITS DURING THE AUSTRAL BREEDING SEASON IN THE SOUTH AMERICAN TEMPERATE FOREST

Abstract

Knowledge of a bird's moult pattern can be useful in the aging of birds. In most North American and European passerines the moult from juvenile to adulthood does not involve all feathers and therefore second year birds can be aged by these limits of the moult. However, it is not yet known whether this approach to aging birds could be applied to Southern Hemisphere passerines. Although most North American and Europe passerine species share similar moult patterns very little is known about the moult patterns in the Southern Hemisphere. I report here on the moult patterns in eight species of southern South American passerines. I also studied the moult patterns of juveniles. Our results indicate that species inhabiting comparable high latitudes in the Northern and Southern Hemispheres have similar moulting patterns. Because the Southern Hemisphere birds used in this study have evolved from tropical desendents, this indicates these patterns are influenced strongly by the environment.

***Key words**:* Moult limits, moult, Chile, Navarino Island, passerines

Introduction

Moult is an essential component of the annual cycle of birds because worn feathers detrimentally affect thermoregulation, waterproofing, courtship display, dermal parasite infestation, flight and ultimately, survival (Ginn and Melville 1983, Debruyne *et al.* 2006). Birds use moult to replace worn feathers or, in some cases, to change plumage (Heise and Rimmer 2000). Moult is controlled by hormones in some avian species (Payne 1972) and cued by the environmental changes in others (Keast 1968). Because the timing of moult rarely overlaps with other activities such as reproduction and migration, moulting is often viewed as costly in terms of energy (Yuri and Rohwer 1997, O'Hara *et al.* 2002). The costs of moulting are known to be high in temperate-zone birds (Murphy and King 1992). During moult, a large fraction of the avian body protein is expended in feather production. Moulting also temporarily reduces a bird's ability to fly, which can enhance the risks of predation (Slagsvold and Dale 1996).

The order Passeriformes (perching birds) comprises over half the species of birds in the world. In passerines of the temperate zones of Europe and North America the adult prebasic (replacement of feathers) moult occurs just after the completion of breeding from July to September or on the wintering ground in the case of some migrants (Jenni and Winkler 1994, Pyle 1997b). Experiments have shown that birds that were moulting while raising young at the same time were not as successful as adults that were not moulting while raising young (Svensson and Nilsson 1997). In eastern North America most adult passerines replace their flight feathers before they migrate and while still on the breeding grounds (Voelker and Rohwer 1998). However in western North America adult passerines typically begin their fall migration before commencing moults (Pyle 1997b). In theory this allows these western species to avoid late summer droughts that frequently occur in western North America (Voelker 2000, Rohwer *et al.* 2007). In Europe the passerines that migrate farthest south often have their complete moult only after reaching their wintering grounds (Ginn and Melville 1983).

In the past it has been assumed that the birds of the Southern Hemisphere have different moult schedules due to the more variable climates experienced in this region (Pyle 1997, Pyle *et al.* 2004). Few data exist on moulting in birds south of the United States border (Pyle 2006). Except for detailed studies in the Rufous-collared Sparrow (*Zonotrichia capensis ssp.*) (Miller 1961, Wolf 1969, Davis 1971, King 1972, King 1976) and three species of Amazonian manikins (Ryder and Durães 2005), only recently have scientists begun to document moult in South American birds (Eisenmann 1959, Lanyon 1975, Short 1976, Oniki 1981, Cikutovic and Guerra 1983, Dyrcz 1987, Peris 1990, Mallet-Rodrigues *et al.* 1995, Oniki and Willis 1999, de Melo 2000, Piratelli *et al.* 2000, Marini and Durães 2001, Capllonch and Lobo 2005, Mallet-Rodrigues 2005, Rickleffs and Shea 2007, Echeverry-Galvis and Córdoba-Córdoba 2008). Most birds in the neotropics can breed all year around and will have as many as three clutches in a year (Foster 1974, Martin 1996). They will often start moulting after the chicks have fledged but if conditions are favorable they will start a new round of breeding and suspend their moult until the new clutch has fledged or moult while breeding if the food supply is adequate (Davis 1971) . This also holds true for birds in temperate Australia and Southern Africa (Payne 1969, Foster 1974, Navarette and Jimenez 1997).

Dwight (1900) first developed the idea of using the difference between juvenile and adult plumages to age birds. The use of moult patterns for aging and its current wide use in the Northern Hemisphere were furthered by Jenni and Winkler (1994) in Europe, and Mulvihill (1993) and Pyle (1997a,b) in North America. Boundaries between retained and replaced wing coverts are termed "moult limits" (Pyple 1997a,b) and can be used to differentiate second year birds from older birds. In general, over half the birds mist netted in any study are either first or second year birds. The difference in juvenile and adult plumage, combined with the ability to use the limit of the first year moult to age second year birds, provides an important tool for the aging of many birds. However, since Southern Hemisphere birds are thought to have a much more varied and complex moulting schedule, the technique of using moult limits to age a bird has not been applied south of the equator

(Pyle 1997b). The lack of knowledge about moulting in southern-temperate birds has hampered further research (Pyle *et al.* 2004, Pyle 2006). Recent publications on Southern South American birds give no examples of the possibility of using moult limits to age birds as none are currently known (Ridgely and Tudor 1994, Azpiroz 2003, Rozzi *et al.* 2003, Couve and Vidal 2004, Martínez and González 2004, Jaramillo 2005). In South America many juveniles delay the moulting of their often female-like plumage for extended periods (Ryder and Durães 2005). This limits our understanding of population demographics, survivorship and age structure in these species. The importance of developing field techniques for the ageing of birds in the hand cannot be over emphasized.

Studies of the speciation of New World passerines are continuing (van den Elzena *et al.* 2001, Joseph *et al.* 2004, Klinka *et al.* 2007, Ohlson *et al.* 2007, Rheindt 2008). Only two species in our study (*Troglodutes a. chilensis* and *Zonotrichica c. australis*) appeared to have evolved from species that originated in the Northern Hemisphere and are only recently separated from the other species in their genus (Rice *et al.* 1999, Ricklefs 2002). A molecular study of the tribe Thraupini found that *Phrygilus patagonicus* and has radiated less than 6 mya from either North or South America and have a complex phylogenetic history (Klinka *et al.* 2007). Among the Tyrannidae, *Elaenia* radiated 12 mya, *Anarietes* radiated 3-4 mya and *Xolmis* 4 mya (Ohlson *et al.* 2007). The Turdinae radiated 7-8 mya and the South American *Turdus* separated from Northern Hemisphere *Turdus* around 4 mya (Klinka *et al.* 2005, Voelker *et al.* 2009). The Furnariidae, containing *Aphrastura. s. spinicauda* are a South American family of an unknown but ancient lineage (Irestedt *et al.* 2006).

The forest of southern Chile and Argentina is separated by over 1000 kilometers from the next nearest forest and has been isolated from other forest biomes since at least 25 mya

(Hinojosa *et al.* 2006). Four of the species in the present study evolved from tropical South American species and the other four are either descended from South American birds that have spread to higher latitudes or are Northern Hemisphere birds that have expanded into South America. Vuilleumier (1991) found a high amount of speciation occurring in Patagonia. As the glaciers started to recede 14,000 ya from southern South America only a few species of birds successfully exploited this new enviroment (Vuilleumier 1991). If it were found that only species capable of altering their moulting pattern to adjust to an ecosystem with a winter season could recolonize this area, it would help explain why so few species have colonized this new environment.

We conducted this study to answer the following questions: When do these species moult? Do they partition the energy needed to reproduce, migrate and moult by performing these functions at different times? Do juveniles have only a partial first moult and if so, can this be used to age one and two year old birds? If, unlike their tropical congeners, temperate forest passerines in both the Northern and Southern Hemisphere have the same moult strategies, what does this say about the role of ecology in selection pressures leading to speciation?

Methods

Since 1999 the Omora Foundation has been conducting a mist netting operation in Omora Park, Navarino Island Chile. Birds have been netted and banded monthly at two locations inside the park with periodic mist netting occurring on other parts of the island (see Anderson and Rozzi 2000, Anderson *et al.* 2002 for a description of study site and methodology). The following species were examined: the migrant White-crested Elaenia

(*Elaenia albiceps chilensis*), the partial migrant Rufous-collared Sparrow (*Zonotrichia capensis australis*) and House Wren (*Troglodytes aedon chilensis*), and the resident Thorn-tailed Rayadito (*Aphrastura spinicauda spinicauda*), Tufted-tit Tyrant (*Anairetes parulus lippus*), Fire-eyed Diucon (*Xolmis pyrope pyrope*), Austral Thrush (*Turdus falcklandii magellanicus*), and Patagonian Sierra-Finch (*Phrygilus patagonicus*). Another species, the Black-chinned Siskin (*Carduelus barbata*), was not caught in large enough numbers to study moult but moult limits were examined.

The primary study site was located in Omora Park on the north end of Navarino Island, Chile (54°57′S 67°39′W). Additional sites were at Guerrico River, Mejillonés River and the alpine zone on Robalo Mountain, all are also on the north side of Navarino Island. The Robalo Mountain site was at an altitude of 535 meters and the others were all at 15-90 meters above sea level. Robalo Mountain was 3.4 kilometers south of the Beagle Channel. The other sites were all 120-840 meters south of the Beagle Channel. Mist nets were operated from 6 to 12 days per month. All birds caught in mist nets from October through May of 2004 to 2006 were checked for signs of primary and secondary wing and lesser, median and greater covert moult. Birds were not examined June though September (winter). Nest searches were conducted on a random basis as time permitted (Table 9). For reproductive phenology I pooled data across all five years because our sample sizes were too small for individual species analysis and I was interested only in looking at general trends (Auer *et al.* 2007)

The primaries were numbered from proximal to distal P1-P9 (or if 10 primary oscines to P10), and the secondaries, S1-S9, from distal to proximal (Pyle 1997b, McGehee and Eitniear 2006). The right wing was extended outward and feathers scored (Gosler 2004).

Head, tail and body moult was not investigated (Table 8). Birds moulting in only one wing were not used in this study. All data from the three years was separated into months with data from the same months across years being combined (Figure 8,9). Recaptured birds were checked only if the recapture was at least 31 days later.

As most of the habitats were homogeneous they were combined together. The only different type of habitat was the alpine zone on Robalo Mountain where 17 birds of 3 species (*E. a chilensis, T. a. chilensis, Z. c. australis*) were caught. None of these species nest in this alpine zone. All eight species have uninterrupted ranges from Santiago to the Cape Horn region (Jaramillo 2005).

Among the eight species in this study only *T. f. magellanicus,* and *P. patagonicus* are sexually dimorphic. *Aphrastura. s. spinicauda* does not show dimorphism in plumage and cannot be sexed because both male and females have a brood patch (Moreno *et al.* 2007). During the course of the study eleven adult *P. patagonicus* and one non-target species (*Carduelis barbata)* in full male plumage were found to have incomplete to fully developed brood patches. Although research has shown that in all but one North American passerine, the male does not develop a brood patch (Pyle 1997b), more work needs to be done in austral birds before the presence or absence of a brood patch could be used to indicate the sex of a bird in the hand. Therefore birds were not sexed in this study.

Terminology mostly follows Pyles (1997b) descriptions. However some of this terminology is inappropriate for Southern Hemisphere birds because these birds hatch in October through January, so on January 1 some are only a few weeks to three months old. In this study juveniles are birds in their juvenile plumage before the first prebasic moult.

Immatures are defined as birds in first-basic plumage in their first calendar year. These are birds between their first prebasic moults to the end of their first calendar year of September 1 and are designated HY (hatch year). Adults are birds that are in their second calendar year, i.e. the year starting in September when birds are old enough to reproduce. These birds are designated AHY (after hatch year). These adults are in either their alternate plumage or prebasic plumage and about to undergo prebasic moult.

Results

Birds examined in this study indicate that all eight species follow a Northern Hemisphere temperate cycle of moult following reproduction (Figure 7) (Ricklefs 1966). The results also agree with the reproductive pattern seen in eight passerines in the savanna of central Chile (Lazo and Anabalon 1992) and in 17 passerines of the subtropical montane forest of northwestern Argentina (Auer *et al.* 2007). The timing and extent of the first prebasic moult is also comparable to those of sister taxa found in the high latitudes of the Northern Hemisphere (Pyle 1997b). Only *Z. c. australis* showed signs of a possible prealternate moult. Among the other species we only found one (*P. patagonicus*) that had any individuals moulting retrices and coverts in the spring (Oct-Late Dec, Table 8). This indicates that if these species have any first prealternate moult in winter or spring it does not include the coverts and therefore second year birds can be aged by moult limits from the first prebasic moult (Pyle 1997b). Due to the small sample size in dimorphic species we were unable to detect a difference in the timing or extent of male and female moult. In all species, females began to develop a brood patch in October and started to moult new feathers over the brood patch beginning in January indicating that the breeding season had ended (Figure 7).

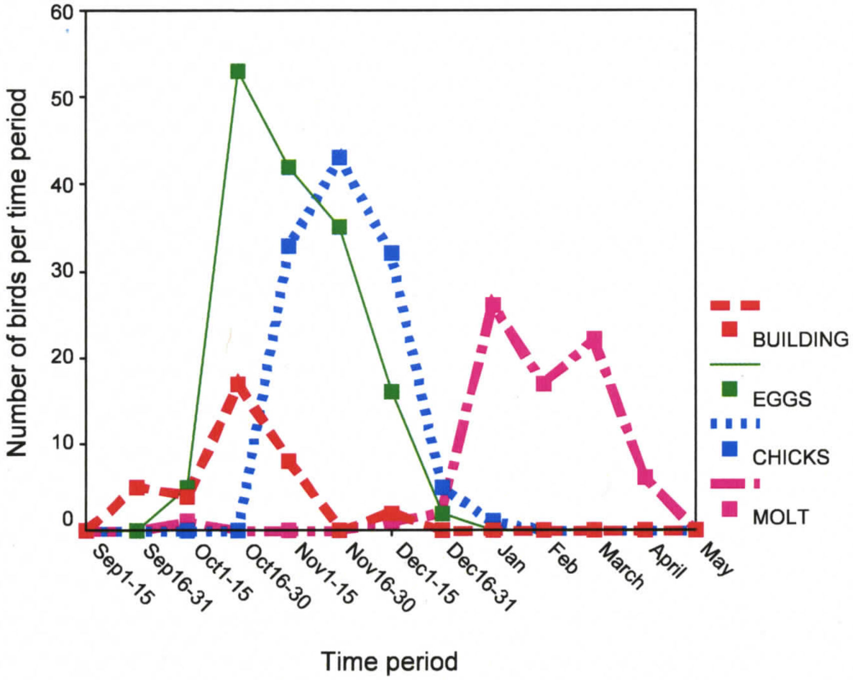

Figure 7: Graph of the phenology of eight species of birds on Navarino Island, Chile. All years and species combined.

Table 8: Number of birds in moult per month for each species. All years combined.

Species	n	# in molt	Sept #	Sept # in molt	Oct #	Oct # in molt	Nov #	Nov # in molt	Dec #	Dec # in molt	Jan #	Jan # in molt	Feb #	Feb # in molt	Mar #	Mar # in molt	Apr #	Apr # in molt	May #	May # in molt
Aphrastura spinicauda	103	5	3	0	20	0	15	0	17	1	9	3	7	0	14	2	7	0	11	0
Elaenia albiceps	227	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anairetes parulus	21	3	1	0	1	0	2	0	5	0	7	1	1	0	1	1	4	1	0	0
Xolmis pyrope	15	5	2	0	2	0	0	0	2	0	1	0	1	1	4	4	3	0	0	0
Troglodytes aedon	96	4	0	0	26	0	7	0	44	0	16	2	3	2	0	0	0	0	0	0
Turdus falcklandii	23	3	0	0	3	0	1	0	4	0	7	2	2	1	1	0	4	0	1	0
Phrygilus patagonicus	276	41	0	0	26	1	63	0	73	2	32	8	19	10	22	15	37	5	4	0
Zonotrichia capensis	56	13	6	0	12	0	9	0	10	0	13	10	3	3	3	0	0	0	0	0
Carduelis barbata	103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	920	74	12	0	90	1	97	0	155	3	85	26	36	17	45	22	55	6	16	0

Table 9: Number of nests encountered on Navarino Island 2000-2005 with dates a nest with an egg was first and last found along with date juveniles were first seen out of the nest.

Species	Number of nests	First nest with egg	Last nest with egg	Date of first juvenile apperance out of nest
Aphrastura spinicauda spinicauda	71	Oct 19	Dec 04	Dec 19
Elaenia albiceps chilensis	1	Dec 20	na	Jan 11
Anairetes parulus lippus	4	Oct 10	Dec 30	Dec 21
Xolmis pyrope pyrope	6	Oct 16	Dec 05	Jan 12
Troglodytes aedon chilensis	22	Nov 08	Dec 14	Dec 18
Turdus falcklandii magellanicus	7	Oct 07	Dec 24	Oct 23
Zonotrichia capensis australis	10	Nov 11	Dec 10	Nov 30
Phrygilus patagonicus	7	Oct 09	Dec 10	Nov 20

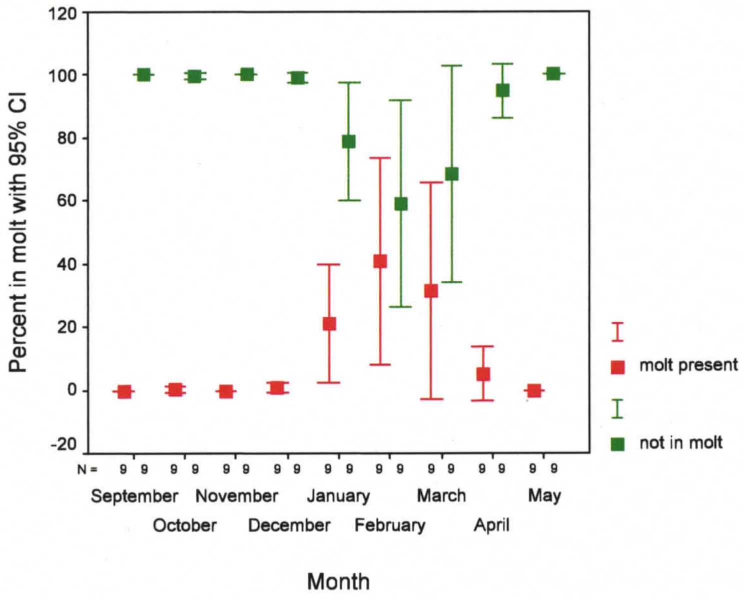

Figure 8: Interval plot with 95% confidence levels of the percent of birds in moult per month on Navarino Island, Chile. All species and years combined.

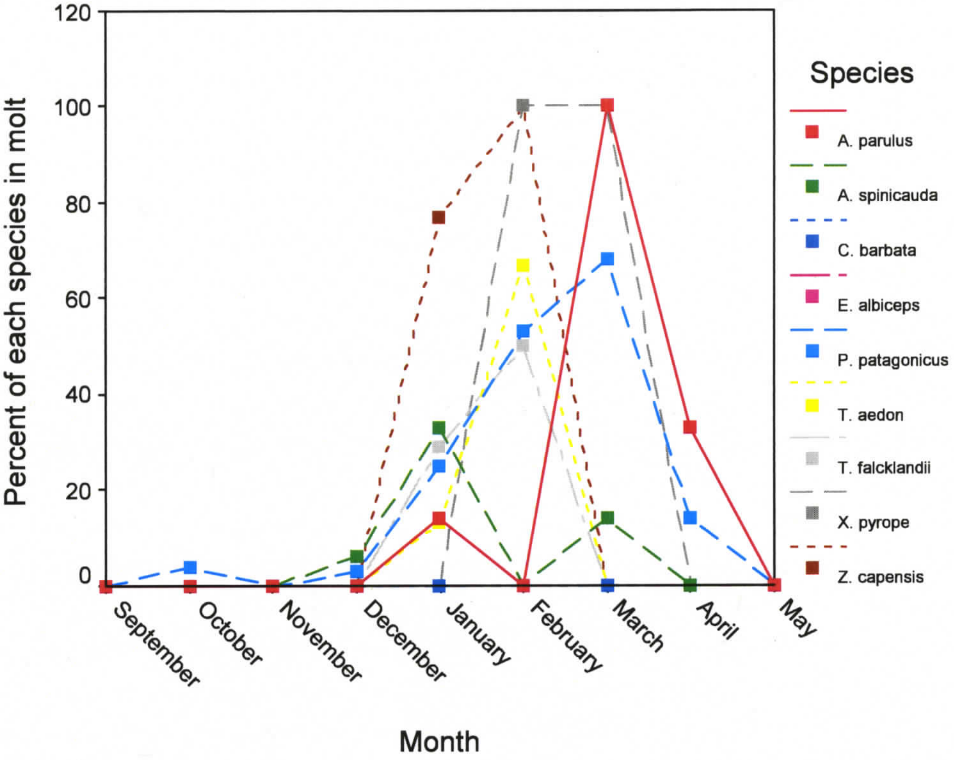

Figure 9: Graph of the percent of birds in moult for each species per month.

Species accounts

Aphrastura spinicauda spinicauda: Five adults showed prebasic moult. One on December 13 was moulting primaries 6 to 8. Three in January were moulting primaries 3 to 8. Two in March were moulting, one was moulting primaries 3 to 5 and one was moulting primaries 1 and 7. No adults in April or May were moulting and all had primaries and secondaries with little or no wear, contrasting with birds in October whose flight feathers were usually worn and duller. No moult was seen in birds in October or November.

Elaenia albiceps chilensis: No moult seen in any birds in the months they were present on Navarino Island (October through April). Flight feathers in adults captured in November and December were worn with especially strong wearing on the lesser coverts. Twelve adults were missing one to three lesser and median coverts but there was no sign of new coverts moulting in.

Anairites parulus lippus: Prebasic moult started in January. Three adults were moulting primaries in January, March and April. Other April and May adults had no moult and unworn feathers. Adults caught in September through December had worn faded feathers.

Xolmis pyrope pyrope: Prebasic moult first seen in February. One adult in February was moulting secondary 1 and primaries 1,4,6,7. In March one adult was moulting secondaries 1,3,4 and 5 and primary 1. A second adult in March was moulting secondaries 1, 6,7and 8 and primary 1. A third adult, possibly a second year bird, in March was moulting secondaries 6 to 8 and some medium coverts.

Troglodytes aedon chilensis: Some juveniles showed a prebasic 1 moult in January and February with the last 1 to 4 greater coverts moulting. In adults prebasic moult starts in January. One adult in January was moulting primaries 1 to 4 and 6 and 7. Another in January was moulting primaries 6 and 7 and the last 3 greater coverts. In February one adult was moulting primary 1 and secondary 1. Another in February was moulting primaries 1 and 2 and secondary 1, 4,5 and 6. By March no birds were seen in moult. In October and November adults had worn primaries and coverts.

Turdus falcklandii magellanicus: Three adult birds were moulting. One in January was moulting some greater coverts and primaries 4 through 7. Another in January was moulting all greater coverts and primaries 9 to 5. In February one was moulting half its median coverts and primaries 1,2 and 9. April and May adults show no moulting and had new feathers whereas October through December adults had worn flight feathers.

Zonotrichia capensis australis: In January one juvenile was moulting greater coverts 1, 2, 6 and 7. In February juveniles moulted all but first 1-3 middle coverts, greater coverts 3-8 and have the red collar starting to come in. In adults the first sign of prebasic moult was in January when birds were moulting in primaries 2 thru 8, with most birds moulting at least primaries 6 and 7. In February primaries 1 through 7 are moulting. Moult appeared to be complete by March although not enough birds were sampled for a conclusive judgment. No birds were seen on Navarino Island after March and were presumed to have migrated north. Adults had worn primaries and showed a few missing greater and median coverts in October thru December which could be a prealternate moult or simply a loss of a few feathers. There was no sign of new coverts coming in until January.

Phrygilus patagonicus: Juveniles, with no start of prebasic 1 moult, seen as late as April 17. In February juveniles often mouled most or all lesser coverts and medium coverts and usually secondary coverts 9 and 8. In March all lesser and medium coverts were moulting. Also greater coverts 9 and up to 4 were moulting in with most moulting just coverts 9 through 7. In April and May over half the juveniles had anywhere from all greater coverts to greater coverts nine through five moulting or moulted in.

In adult *P. patagonicus* prebasic moult was first seen February 23 and still occurred by April 25. One SY male was moulting greater coverts and secondary 1 (possible alternate 1 plumage?) on October 6. Prebasic plumage starts in late December with 1 adult male moulting primaries 3-1 and one adult female moulting primaries 1 to 5. In January birds generally start moulting primaries 3 and 4 and then up to 9. In February more are moulting 7-9. Primary 1 was only seen moulting in April. All adults were finished with moult by May. Usually the primary coverts are moulted at the same time as their corresponding primary feathers.

In a ninth species *Carduelis barbata* there were not enough birds in moult to reach any conclusions, but there was clearly only a partial prebasic moult in juveniles, which allowed for the discrimination between second year and older birds.

Discussion

These results represent the first significant attempt to analyze moult patterns in Southern South American passerines. From the data presented it is now possible to estimate individual ages to second year and in some cases, even after the second year, by using the condition of feathers and moult limits. This information, which is consistent over four separate families, suggests that this technique is likely to be of general use with other Southern South American passerines. These results are consistent with the recent work by Ryder and Durães (2005) who demonstrated that moult limits could be used to age three species of Neotropical Manakins (Pipridae). Our work contributes to the growing body of literature (Pyle *et al.* 2004, Pyle 2006) that at least in the New World there are numerous species of birds that have similar moulting patterns and each species and subspecies should be studied to confirm its moult patterns and thereby the possibility of aging birds by moult limits.

Species accounts

Aphrastura s. spinicauda shows a moulting pattern corresponding to ecologically similar bark gleaning, cavity nesting species in North America (Pyle 1997b). This is somewhat surprising considering this species comes from an ancient family of South American origin. On Navarino Island, *A. s. spinicauda* nests from October until January with eggs seen from October 19 until December 4. Chicks are still in the nest as late as December 16. The Furnariidae is a strictly South American family with very little published on moult. In Brazil, Bugoni *et al.* (2002) found 3 species of Furnariidae that moulted at the end of the breeding season and five species that had an erratic moult. The moult of *A. s. spinicauda* is one of the longer in Southern South American passerines. This could be because of the Rayadito's prolonged parental care (Moreno *et al.* 2005). Moult limits were not conclusively seen but probably exist in this species. More study must be done with banded juveniles.

Elaenia albiceps, a Tyrannid, is found from southern Colombia and eastern Brazil to the Cape Horn region of southern Chile (Ridgley and Tudor 1994, Rozzi *et al.* 2003). It is often divided into 5 subspecies with one, *E. a. chilensis*, considered migratory (del Hoyo *et al.* 2004). Based on the study of 39 museum skins collected in the winter and 44 in the summer, Zimmer (1941) stated that *E. a. chilensis* moulted on its wintering ground in Peru, Bolivia, Colombia and Brazil. The results of the present study concur with the conclusions of Zimmer (1941).

On Navarino Island, one *E. a. chilensis* nest with an egg was found on December 27, 2000 and one bird was seen carrying a twig in its beak on November 16, 2004. The first juvenile *Elaenia* seen out of the nest was between January 3 and February 4 each year. This indicates that *Elaenia's* on Navarino may nest as early as the third week of November. During a five-year period the last adult *Elaenia* was seen or heard between February 13 and April 7 with most gone by mid March (Brown *et al.* 2007, McGehee unpublished data). *Elaenias* were first seen on Navarino on October 14. However, if most lay from mid December to mid January and migrate out by the middle of March, then they have at most 60 days, and more likely fewer days, to complete their moult before they migrate. Passerines take an average 60 to 80 days to complete flight feather moult (Ginn and Melville 1983). This would indicate that it is much more advantageous for *Elaenias* to wait and moult on their wintering grounds.

There are 36 species of Tyrannidae listed by Pyle (1997b) as inhabiting the United States and Canada. Adults of 13 species in this family moult their flight feathers on their summer grounds. Of these 13 species that show a moult on their summer grounds, eight are year round residents or migrate only a short distance. The rest either have a total or partial flight feather moult on their respective wintering grounds. This study of *E. a. chilensis* confirms that this Southern Hemisphere Tyrannid conforms to the pattern seen in the Northern Hemisphere. A study in Brazil (Bugoni *et al.* 2002) found five species of Tyrannid moulted at the end of the breeding season while six species had an erratic moult pattern.

The subspecies *E. a. albiceps* breeds in northern Argentina and migrates to a different area of Brazil than *E. a. chilensis*. Its wintering grounds are much closer, but it too moults its flight feathers on the wintering ground (Capllonch and Lobo 2005). One specimen of *E.*

albiceps in Brazil was found moulting its wing feathers at the end of the breeding season (Oniki and Willis 1999). Another closely related species, *E. strepera*, spends only 3 months on its breeding grounds in Northern Argentina and it also moults only on its wintering grounds in northern Peru and Southern Colombia (Capllonch and Lobo 2005). In Panama, where a resident and migratory *Elaenia spp.* overlaps, the migratory *Elaenia* has great synchrony in reproduction (Stutchberry *et al.* 2007), much like *E. a. chilensis*. However, their moulting patterns are undescribed. The family Tyrannadae has unpredictable moult strategies in the tropics (Bugoni *et al.* 2002), but not enough data have been collected on other members of the tropical genus *Elaenia* to make any firm conclusions.

The two species with the fewest data, *A. p. lippus* and *X. p. pyrope*, still show a pattern of moult that corresponds to species inhabiting similar niches in the Northern Hemisphere (Pyple198b). Nests of *A. p. lippus* were encountered from October until January and juveniles were first seen on December 21. *Xolmis. p. pyrope* nests from October until December (McGehee unpublished data). In the closely related *X. irupero* of Brazil, molting appeared to occur during the breeding season (Bugoni *et al.* 2002). These two species are members of the family Tyrannadae, known for having unpredictable moult strategies in the tropics and predictable strategies in the northern temperate latitudes (Pyle 1997b, Bugoni *et al.* 2002). Not enough juveniles were caught to document moult limits in these two species, but a few adults caught in October and November had different amounts of wear on their coverts, indicating probable incomplete post juvenile moult and therefore moult limits might be used to age SY birds.

We were unable to detect moult limits in *Troglodytes a. chilensis*, which corresponds to what was found in the North American subspecies of *Troglodytes aedon spp* and other

Troglodytes (Pyle 1997b). The breeding and moulting season of *T. a. chilensis* in this study is similar to northern latitude *Troglodytes* (Pyle 1997b). *Troglodytes a. chilensis* nested from October until December and were on Navarino Island from September to April (McGehee unpublished data). In Monteverde, Costa Rica, Young (1994) found most *T. aedon* raising two broods between March through July and then moulting in September and October when juveniles started dispersing. In the present study no birds were mist netted in May through September; however, a few birds were seen in all months of the year, usually in vegetation near houses (McGehee and Arango pers obs.). The possibility exists that Southern Chilean birds have a post breeding dispersal similar to that which occurs in *T. aedon* in North America (del Hoyo *et al.* 2005), where the moult continues into autumn. Birds mist netted in October through December had worn feathers, indicating no prealternate moult. More study is needed to define moult limits in this species.

Because it originated in a high northern latitude, *T. aedon* is an example of a species that originally had a high latitude moulting strategy. As this species gradually moved south into mid latitudes and the equator, its phenotypic plasticity in regards to moult allowed it to shift its moult schedule as the opportunity for multiple clutches in a season increased. But as it reached the bottom of South America it reverted back to a typical Northern Hemisphere high latitude moult schedule.

Turdus f. magellanicus nests on Navarino Island from September until December. Juveniles had medium coverts that were white tipped and less overall strong brownish colour than adults. More juveniles need to be captured to confirm this but it should show up in spring second year birds as a moult limit. In the Northern Hemisphere, juvenile thrushes in the genus *Turdus* are known to have a partial prebasic moult and therefore can be aged by moult limits (Simms 1978, Pyle 1997b). *Turdus f. magellanicus* exhibits the same moult strategies as northern latitude thrushes (Ginn and Melville 1983, Jenni and Winkler 1994, Pyle 1997b). In Brazil Bugoni *et al.* (2002) found two species of *Turdus* that moult all year round and one species that moulted 2 months after the breeding season was over. In Northwestern Argentina temperate forests between 20º-30ºS, Capllonch *et al.* (2008) found *T. n. nigriceps* to follow the Northen Hemisphere pattern of moulting after the breeding season, which starts a month later than at my study site.

Phrygilus patagonicus is found only in the forests and forest edges of Southern Chile and Argentina (Rozzi *et al.* 2003). The eleven species in the genus *Phrygilus* are restricted to South America. Nothing is known about their moult. *P. patagonicus* nests with eggs between October 9th and Decemebr 10th (McGehee unpublished data). *Phrygilus patagonicus* follows the moult pattern of other Thraupids and ecologically similar species in North America, all of which are migrants (Pyle 1997b). In the same family in Brazil, Bugoni *et al.* (2002) found 13 species that showed similar patterns to *Phrygilus patagonicus* and seven that showed erratic moult patterns. Juveniles had a definite partial prebasic moult. This combined with the striking difference in colour between juveniles and adults feathers mean that moult limits can be used to easily age second year birds in this species.

Zonotrichia capensis is found from Mexico to Cape Horn and its moult has been studied in the sedentary subspecies from Costa Rica to Argentina (Miller 1961, Wolf 1969, Davis 1971, King 1972). On Navarino Island, *Z. c. australis* nests had eggs from Novemebr 5th to December 12th. . They are present on Navarino Island from September until March. Therefore the possibility exists that moult continues during migration. Birds arriving on their breeding grounds in September and October showed no sign of new feathers having been moulted in during the winter as all feathers were worn and faded. Some birds appear to migrate as far north as Bolivia while others remain year round (Chapman 1940, Couve and Vidal 2003). Large numbers are seen at the north end of Tierra del Fuego Island and the corresponding mainland coast 250 to 325 kilometers north of Navarino Island in April and May (S. McGehee unpublished data, S. Imbroglio pers. comm.). Chapman (1940) reports they have been seen year round in Santa Cruz and Tierra del Fuego Island.

In Brazil, *Z. capensis* was found to moult after the breeding season (Bugoni *et al.* 2002). In Colombia, Miller (1961) found that *Z. c. costaricensis* undergoes two complete moults a year, corresponding to the rainy seasons. In Costa Rica, Wolf (1969) found that *Z. c. costaricensis* adults had a prealternate moult of inner secondaries overlapping with breeding. Their prebasic moult came after breeding during the rainy season. In Panama, Kalma (cited in King 1976) stated that the nesting season was often followed by a partial wing moult, then all birds had a complete flight feather moult. In the coastal desert of Peru, Davis (1971) found that although *Z. c. peruviensis* moulted right after the breeding season, many adults had a second moult just before the start of breeding season involving 2-6 primary feathers, the opposite of that found in Panama. In the Chaco region of northwestern Argentina, King (1972) found no prealternate moult in *Z. c. peruviensis*. One-fourth of the lowland birds suspended their moult in response to possible renesting. As summarized by King (1976) the data from five different parts of Central and South America indicate each subspecies moult is controlled by local environmental conditions. Peris (1990) found all 13 of the *Z. capensis* he mist netted in Paraguay in December to be in moult with none showing signs of reproduction, indicating that they, like the birds in this study, moult after the breeding season, which comes earlier in Paraguay. Like the other subspecies in this study having a range from Cape Horn to

Mexico (*T. m. chilensis*), this species has the ability to alter its moult strategy to minimize overlapping energy-demanding events in its life cycle. Although most subspecies of *Z. capensis* cannot be aged with moult limits because their moult pattern is erratic (Miller 1965, Wolf 1969, Davis 1971, King 1979), my study of the austral subspecies shows a moult pattern similar to North American *Zonotrichia*, with the few juveniles captured showing only a partial prebasic moult. Chapman (1940), in a study of all subspecies based on museum skins, proposed that first year birds moult all their wing covert feathers but we found that they have only a partial covert moult.

Z. capensis is an example of a species that probably started out with a high latitude moulting strategy. As this species slowly moved south into mid latitudes and the equator its phenotypic plasticity with regard to moult allowed it to shift its moult schedule as the opportunity for multiple clutches in a season increased. But as it reached the southern latitudes of South America it reverted back to a typical Northern Hemisphere high latitude moult schedule due to environmental constraints imposed upon breeding.

Four of these species (*Zonotrichia capensis australis*, *Carduelis barbata*, *Turdus falcklandii magellanicus*, and *Phrygilus patagonicus*) showed clear evidence of only partial prebasic moult in the coverts of juveniles. The other five species did not show definitive evidence of partial prebasic moult, but preliminary evidence indicates that future research may uncover that other five species have partial first year moults (*Anairetes parulus lippus*, *Xolmis pyrope pyrope*, *Elaenia albiceps chilensis, Troglodytes aedon chilensis* and *Aphrastura spinicauda spinicauda*). This pattern has also recently been found to hold for Cuban birds (Pyle *et al.* 2004). It took over 100 years of research to confirm that moult limits could help age 252 out of 288 North American passerine species in the hand (Pyle 1997a).

Whether or not the pattern is available to help age neotropical species has not yet been adequately studied. Future research may indicate that most of the world's passerines species do not have a complete prebasic moult and therefore can be separated into juvenile, second and after second year birds when examined. However if this is true in tropical species, they may still not be able to be effectively aged by moult limits as they often have an unpredictable moult schedule (Pyle 1997b).

Implications

In birds the breeding season usually corresponds to the period of maximum food availability (Davis 1971) and then is followed by moult. This is because most birds are not able to raise young and moult at the same time. Consequently how to partition these events is a challenge for any species. Moult also compromises thermoregulation as birds in moult have a reduced capacity to insulate themselves against temperature change and moisture (Davis 1971). On Navarino Island all of the avian species in this study lay their eggs during the time of increasing photoperiod (Oct-Dec) and raise their young during maximum photoperiod (Nov-Jan). The fledging period corresponds to maximum fruit and seed production of most Navarino Island plants (McGehee, unpublished data). It is also the time of highest insect abundance (McGehee, unpublished data). Southern South American birds thus demonstrate reproductive seasons parallel to birds inhabiting similar latitudes of North America and Europe.

In addition to refining moult limits and defining moult strategies for each species, there is also the need to understand the underlying ecological factors controlling moult. On the island of Dominica it has been shown that moult will vary within a species and is occasionally interrupted in some individuals (Diamond 1974). In Costa Rican rain forests, Foster (1975) found that 20% of the 47 species examined displayed an overlap of moult and breeding. On the Galapagos Archipelago, where there is not a marked seasonality in weather, *Progne modesta modesta* breeds and moults at the same time (Eisenmann 1959).

Brazil is the one neotropical country for which a few moult observations have been published. Marini and Durães (2001) found that birds inhabiting the drier parts of Brazil had their moult controlled by the cycle of rain, whereas Foster (1974) found the higher overlap between moult and reproduction in tropical Brazil was caused by the prolonged tropical breeding period. The Brazilian passerine *Ramphocelus bresilius*, which inhabits dry scrubby brush land, was found by Mallet-Rodrigues *et al.* (1995) to have a post-juvenile moult that was highly variable. They also found the adults moulted for six months out of the year. In a forested area of southeastern Brazil with heavy rainfall, Mallet-Rodrigues (2005) found that moult and breeding did not overlap in 56 species of passerines, although moult proceeded more slowly than in the present study, lasting about four months. Piratelli *et al.* (2000) observed moult in 14 localities in Mato Grosso Brazil, in a tropical climate with a pronounced dry season. They found that breeding corresponded with the start of the rainy season and there was no overlap between reproduction and moult. In the Cerrado semi-deciduous forest of Brazil, Bugoni *et al.* (2002) found that moult in 55 species occurred predominantly at the end of the breeding season with some overlap and a prolonging of the moult period. Also a number of species were shown to be moulting in most months of the year.

During the last few years the plasticity of moult has become widely established (Flinks *et al.* 2008). Consequently, if environmental changes occur this could cause a subpopulation to be forced to adapt by changing their moult pattern. A different moult pattern can lead to different feather colours during the breeding season and this could further the possible speciation of the subpopulation (Flinks *et al.* 2008), especially if females have a preference for certain colours in males. There is some evidence that differences in moult between different genotypes mating at a hybrid zone reduce hybrid fitness (Voelker and Rohwer 1998, Carling and Brumfield 2008). Southern Chile and Argentina have at least 73 species of birds showing signs of speciation that can be traced to the last ice age (Vuilleumier 1991). Twenty-five species have overlapping hybrid zones and may not have yet attained full speciation. Only 7% (16 of 217) appear to be relict species that were present before the last glaciation (Vuilleumier 1991). Most of the species now inhabiting Southern Chilean forests are believed to derive from species that spent the last ice age in warmer areas where they may have had a tropical moult pattern. Perhaps only if they had the phenotypic plasticity to shift their moult pattern, could they successfully immigrate to a higher latitude. If those species immigrating to high latitudes are forced to change their moulting schedule, this could be one of the factors that has led to speciation (Martin and Tewksbury 2008) and needs to be investigated further. It could also explain why only a few species have so far colonized the higher latitudes of South America after the last ice age.

The widespread existence of ecogeographical patterns is evidence of a species' ability to adapt to fluctuating environmental conditions (Millien *et al.* 2006). The connection between developmental plasticity and speciation has become well known (Kondo 2008). Different phenotypes will appear in response to changes in the environment, which can lead to speciation. These adaptive responses of species to current environmental conditions appear to be independent of ancestry (Diniz-Filho *et al.* 2007). However there are still doubts that ecological speciation is prevalent in birds due to a lack of examples (Edwards 2008, Price 2008). Finding general patterns in ecology and evolution along with their exceptions is the first step to uncovering the processes that shape them (Ashton 2001). There is perhaps no single explanation for these patterns, but the importance of studies confirming or rejecting ecological rules has been emphasized repeatedly (Gaston *et al.* 1998a,b, Adams and Church 2008). Our results indicate that there is a widespread occurrence of similar moulting patterns at high latitudes. This could be caused by the same ecological factors acting on natural selection at high latitudes, and this may be an example of an ecological rule.

Ricklefs (2006a) recently emphasized, "The distribution of each species reflects its adaptations with respect to physical factors in the environment and biological agents. Although the status of a particular species at a given time would be difficult to predict, its distribution through a region is more the product of deterministic processes of population interaction than of a random walk. Thus, we should think of ecological systems as being relatively stable with respect to parameters that change continuously." This study will hopefully lay the groundwork for future researchers to confirm that southern South American passerines, although isolated from their Northern Hemisphere congeners by many millions of years, have evolved many of the same moulting strategies and should not be lumped in with Neotropical species.

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Chapter V

Summary

Since Darwin's time, the theory that changing ecological conditions resulted in speciation through natural selection has been largely accepted, though only a modest number of data from nature are available to support this model (Schluter 2000). The dominant paradigm is still that species arise primarily through geographic isolation of populations that have diverged due to local ecological conditions (Newton 2003). The role of speciation in adaptive radiation remains unclear. Divergent natural selection caused by ecological speciation may cause a more rapid speciation rate (Schluter 2000). Because birds can fly, they are able to colonize remote areas of the world that other species find difficult to reach (Price 2008), making them an excellent subject for the study of ecological speciation. About a third of southern South American birds show evidence of speciation between the start of the Pleistocene 1.8 Mya, and the present (Vuilleumier 1991). The region of Patagonia that is now forested was almost completely covered in glaciers 18,000 years ago (Markgraf 1989). Therefore the current avian community represents recent colonizers to newly available ecological niches.

Current studies are revealing that reproductive isolation among sympatric populations occurs in birds much faster than previously thought (Wang *et al.* 2003, Grant and Grant 2008). If some avian species have the genotypic ability to alter major life history traits such as body size, fat accumulation or moult they should be better able to colonize newly opened niches. This study has shown that whether my study species ancestors originated in North

America or South American they must have likely carried the genetic capacity to inhabit a temperate climate. However, if by filling these niches they proceed to produce environmentally influenced phenotypes that are unattractive to mates or they render themselves reproductively isolated, then speciation should occur. This is especially true when gene flow is limited, or halted by the same environmental factors.

The results of this thesis, shows that those species colonizing Southern South America after the last glaciation were compeled to adhere to Bergmann's rule and high northern latitude moult strategies due to the environmental conditions. However, the climate was not extreme enough to induce them to adopt a winter fattening strategy as birds commonly do in similar latitudes in North America. This shows that these species adapt and alter their tropical life history strategies only when extreme ecological conditions warrant it.

Kozlowski and Gawelczyk (2002) state that when studying body size distributions in organisms: "We are in the position of an observer watching a chess game without knowing the rules: before the rules are unravelled the game looks chaotic. After the rules are known, it is still amazing that such simple rules can allow so many different outcomes." The goal of science is to produce theories that can then be used to successfully predict behaviours observed in the real world. The results of this thesis, coming from an unstudied continent, add data confirming the universality of ecogeographical rules and further documents the importance of the study of the local ecology. This leads to the realistic possibility that there are yet other equally universal patterns that explain additional properties of ecological systems (Brown *et al.* 2002). The next step is to look for additional ecogeographical patterns and uncover the underlying processes that cause these patterns (Diniz-Filho 2007). Although the conclusions presented here are preliminary, it is hoped that the observations reported in this thesis will serve to encourage other researchers to pursue, in Southern South America, lines of research similar to those already undertaken in North America and Europe. As for myself, I will in the coming years, continue to gather data in South America to further elucidate the ideas presented in this thesis.

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Appendix A

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