

**LIFE HISTORY AND ENVIRONMENTAL CORRELATES OF SURVIVAL RATES IN
TROPICAL BIRDS**

by

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Abstract

Current thinking suggests that survival, and consequently lifespan of organisms, can be understood in terms of trade-offs between self-maintenance and reproduction, and constraints imposed by physiological mechanisms, such as metabolic intensity. While comparative studies show that many life history traits covary predictably with climate, few studies have examined variation in survival across latitudinal or elevational gradients. I paired survival rates with reproductive, morphological, behavioral, and physiological traits, as well as environmental variables to quantify the intrinsic and extrinsic drivers shaping avian life histories. In Chapter 2 I ask whether tropical birds around the world are longer lived than their temperate counterparts. My results suggested an inverse relationship between latitude and survival in the northern hemisphere, but this pattern is dampened or absent for the majority of southern hemisphere species. I also showed that extrinsic factors related to climate were poor predictors of survival compared to latitude alone, and that the relationship between survival and latitude is strongly mediated by intrinsic traits — larger, non-migratory species with smaller clutch size had the highest survival. In Chapter 3 I focus within the Neotropics to examine how a basic physiological trait (basal metabolic rate; BMR) is linked to survival of montane and lowland birds. I found that lower BMR predicted higher survival, regardless of the elevation at which species occurred. In addition, elevation had a direct negative effect on survival, perhaps due to harsher abiotic conditions, low site fidelity, or both at higher elevations. To help facilitate estimates of age-specific survival in future studies, I determined the molt ageing criteria for South American manakin species in Chapter 4, which can be used to distinguish juveniles from adults. Like many temperate species, the occurrence of a partial preformative molt allowed

separation of age classes based on the presence of molt limits. By drawing on both variation within the tropics and across birds globally, this dissertation provides new evidence of the connections between the high survival rate of tropical birds, their life history traits, and the environment.

Lay summary

Why do some species live longer than others? In this dissertation I look at how differences in life history traits and the environment impact avian survival, and hence, lifespan. I showed that the longest-lived bird species are those with large body size that lay fewer eggs. I also found that survival is generally higher for birds from tropical ecosystems, and that this effect is strongest in songbirds. I go on to demonstrate that the lower energy metabolism of species inhabiting tropical rainforests, which are warmer and less seasonal than northern latitudes, may help explain the higher survival of birds living near the equator. To help facilitate estimates of age-specific survival in future studies, I determined the molt ageing criteria for South American manakin species, which can be used to distinguish juveniles from adults.

Preface

The dissertation work presented here is based on original and independent research by the author, Micah Noel Scholer.

Work for Chapter 2 was conducted in collaboration with Matt Strimas-Mackey. I conceived the ideas, designed methodology, collected data, conducted analyses and wrote the paper. Matt Strimas-Mackey assisted with the analysis and delineating species ranges using eBird data. Jill Jankowski contributed ideas during the design and write-up phase.

A version of Chapter 3 has been published: **Scholer, M.N.**, P. Arcese, G.A. Londoño, M. Puterman, and J.E. Jankowski. 2019. Survival is negatively related to basal metabolic rate in tropical Andean birds. *Functional Ecology* 31: 1436–1445. I conceived the ideas, designed methodology, collected field data on survival between 2014–2016, conducted statistical analysis and wrote the paper. Gustavo Londoño and Jill Jankowski collected data on survival and basal metabolic rate from 2011–2013. Martin Puterman helped analyze the data. Jill Jankowski and Peter Arcese helped design the study and contributed ideas during the write-up phase.

Work for Chapter 4 was conducted in collaboration with Jeremiah Kennedy and Blaine Carnes. I designed the study, collected data, conducted statistical analyses and wrote the paper. Blaine Carnes and Jeremiah Kennedy helped with data collection and preparing species accounts. Jill Jankowski supervised the study and provided ideas during the write-up phase.

All protocols involving the use of animals in this dissertation were approved by the UBC animal care committee (A15-0067, Species ranges and diversity of tropical birds). Permits to conduct research within South America were obtained through Peru's National Forest and Wildlife Service (SERFOR research permits no. 242-2015, 343-2016).

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Dedication

To my son, Samuel Wilder, in hopes that the natural world that has so captivated me will persist in its greatness for you to ponder as well.

Chapter 1: Introduction

1.1 Background

The idea that plants and animals of different sizes, shapes and behaviors vary in their rates of annual survival must be very old. Aristotle was likely one of the earliest to comment on the subject, noting that larger organisms tended to be longer lived than smaller ones and those that reproduced more frequently aged quicker (Aristotle, 350 BC). Although Aristotle's explanation for these phenomena turned out to be incorrect (he posited that aging, reproduction, and size were related to an animal's water content), his observation that important trade-offs exist among organisms' morphological and life history traits were valid. More than two millennia later, trade-offs between key maturational and reproductive characteristics would take center stage in forming the foundation of one of the most comprehensive analytical frameworks in organismal biology (Stearns 1989) — life-history theory (LHT).

The aim of LHT is to explain the bewildering array of life cycles, or life histories, in existence (Stearns 1992), ranging from extremely small and fast reproducing unicellular microorganisms, such as yeast, to large and long-lived mammals that give birth only once every 3 to 4 years, such as elephants. LHT is based on the premise that phenotypes are composed of life-history traits such as length of life, size and age at first reproduction, and size and number of offspring (Stearns 1992, Roff 2002), and that these traits are modulated by a combination of natural selection and allocation trade-offs to vital biological functions (Stearns 1989). For instance, because resources are limiting, organisms can invest time or energy into either self-maintenance, growth, or reproduction. The variable ways that individuals, populations, or species navigate this dilemma determines their position along a slow-fast continuum of life-histories

(Stearns 1983). At the ‘fast’ end of the continuum are species that invest more in reproduction, and less in self-maintenance, decreasing survival overall; whereas ‘slow’ species display opposite patterns. These life history strategies are coupled to sets of physiological traits, including metabolic, immunological, and hormonal, that have coevolved in response to ecological conditions (Wikelski and Ricklefs 2001, Ricklefs and Wikelski 2002). Furthermore, behavioral traits, such as migratory habit, also play a functional role in mediating life-history trade-offs (Weimerskirch et al. 2015, Sturrock et al. 2015, Satterfield et al. 2018), and thus covary predictably with life-history traits (Réale et al. 2010). In this way, LHT bridges principles of evolution, ecology, behavior, and physiology operating on life-history traits that affect both individual fitness and population dynamics. It is a powerful framework for understanding patterns in the diversity of life histories found across the planet.

A central tenet of LHT is that investing more in reproduction reduces survival (Williams 1966, Stearns 1992, Roff 2002). This pivotal trade-off has been observed across taxa including birds (Ricklefs 1977, Linden and Møller 1989, Ghalambor and Martin 2001), mammals (Ransome 1995, Mills et al. 2010, Dammhahn 2012, Culina et al. 2019), reptiles (Cox and Calsbeek 2010), fishes (Gunderson 1997, Polverino et al. 2018), insects (Gwynn et al. 2005, Marshall and Sinclair 2010), rotifers (Snell and King 1977), plants (Roach and Smith 2020), and even virions (De, Paepe and Taddei 2006). Much of the variation in these two traits track differences in the body size of species (Stearns 1983, Saether 1988, Promislow 1993, Dobson 2007). The example given earlier contrasting life history of yeasts and elephants exemplifies this point. Yet, considerable variation in slow-fast life histories remains unexplained in natural populations even after the effects of body size are removed (Harvey and Zammuto 1985, Read and Harvey 1989, Promislow and Harvey 1990). When body size is controlled for, a new tempo

of life emerges, one which also focuses on a slow-fast continuum in survival and reproduction (Dobson 2007). This second axis of life-history variation is thought to be governed by differences in mortality patterns (Williams 1957, Stearns 1992, Roff 2002), specifically during early life stages (Promislow and Harvey 1990). According to this view, extrinsic sources of mortality mediate the survival–reproduction trade-off — high mortality rates favor investment in reproduction over a short lifespan while low mortality produces species that are long-lived and reproduce less often. Empirical support for this idea is nevertheless mixed (Furness and Reznick 2017), and some evidence suggests that mortality rates and life-history strategies vary along different selection gradients (Tieleman 2009, Hille and Cooper 2015). This raises the need for studies that include macroecological variation to determine whether the survival–reproduction trade-off is a fixed construct or the result of different selection processes (Polverino et al. 2018).

1.2 Environmental variability and the use of climate gradients in life-history studies

Life history strategies are thought to evolve in response to environmental conditions, especially those related to climate (Stearns 1992, Pfister 1998, Smallegange et al. 2014). Temperature, for instance, plays a critical role in determining the rate of biochemical processes, which impact everything from rates of growth and development to organismal performance (Kingsolver and Huey 2008, Kingsolver 2009). Certain aspects of temperature, particularly minimum winter temperature, may also have direct impacts on mortality rates (Robinson et al. 2007, Salewski et al. 2013). Similarly, precipitation can affect animal physiology and mortality through its influence on seasonality of food abundance (Lack 1947, Ricklefs 1980, Roff 2002). Climatic conditions thus impose important constraints on the timing of and investment in reproduction, which in turn affect survival rates and, ultimately, species fitness and distribution (Clarke 2003).

Thus, a useful way to understand how variation in environmental conditions influences survival and reproduction is by studying individuals, populations, and species across sites with contrasting climatic gradients. Differences in the macroecological conditions found across elevational and latitudinal gradients provide an ideal testing grounds for predictions generated by LHT (De, Frenne et al. 2013, Hille and Cooper 2015, Boyle et al. 2016).

As a general rule, mean annual temperature and precipitation both decrease with increasing elevation and latitude (Barry 2008). Other extrinsic factors such as day length change with latitude, but not elevation, whereas ultraviolet radiation and partial pressure of oxygen and other atmospheric gases change with elevation, but not with latitude. Those climatic variables that do change have different rates of spatial turnover along these two types of gradients (Loarie et al. 2009). For instance, one would experience much more dramatic changes in temperature traveling up a mountain slope than over the same distance across latitude. The strength of such environmental gradients has important implications for how individuals experience environmental barriers to dispersal and levels of gene flow between populations (Janzen 1967). Hence, local adaptations to environmental conditions are expected to differ across gradients (Jump et al. 2009, De, Frenne et al. 2013). Understanding the relative importance of different selective pressures in shaping life history strategies therefore requires approaches that explore ecological correlates of life-history trade-offs between both elevational and latitudinal gradients.

Birds are perhaps one of the best animal groups to explore variation in life-history strategies because they are the most well sampled vertebrate organisms (Titley et al. 2017), and comparative studies show that many avian traits vary predictably over climatic gradients. For example, tropical species lay smaller clutches (Lack 1947, Kulesza 1990, Martin et al. 2006, Jetz et al. 2008b), prolong incubation (Martin et al. 2007), are slower to reach sexual maturity

(Martin et al. 2011) and display lower basal metabolic rates (e.g. BMR) than north temperate species of similar body mass (Wiersma et al. 2007b, Londoño et al. 2015, Bushuev et al. 2017). Given this suite of traits, LHT predicts that avian survival in tropical regions should be relatively high to offset lower reproductive output (Martin 1996). However, there remain significant gaps in the empirical support for this prediction, and it has yet to be shown whether avian survival rates covary with latitude worldwide. Illustratively, compared to the northern hemisphere, far fewer studies of survival and reproduction exist for tropical regions and austral latitudes. In contrast to latitudinal gradients, shifts towards slower life-histories and higher survival are generally observed for high elevation bird species (Bears et al. 2009, Tieleman 2009), despite these regions being more seasonal, with pronounced flushes in food availability compared to low elevations (Hille and Cooper 2015, Boyle et al. 2016). These generalizations have largely been extrapolated from studies of mountain ranges in the northern hemisphere, and so suffer the same north-temperate bias reflected in our understanding of life-history variation across latitude. Moving towards a more rigorous assessment of the survival–reproduction trade-off, and one which involves a greater diversity of species and biomes, thus requires examination of the ecological correlates of avian survival from around the globe generally, and within the tropics, specifically.

The goal of my dissertation research is to fill this knowledge gap through a combination of comparative and meta-analytical approaches to examine the ecological correlates of avian survival rates. As such, my thesis aims to understand the morphological, physiological, and ecological drivers of survival for a broad range of avian taxa across different selection gradients. I accomplish this by first examining global trends in survival, body size, reproduction, behavior, and latitude (Chapter 2) and, secondly, by studying variation in survival and physiology in a

tropical elevational gradient (Chapter 3). I conclude by discussing how survival estimates and, hence, our understanding of life-history trade-offs, can be improved by classifying birds into age and sex categories based on patterns of feather molt (Chapter 4). Through this research I provide novel insights into the varying selection pressures acting on survival rates in birds.

1.3 Research conducted for this dissertation

The unifying theme of this dissertation is that survival rates are influenced by a combination of intrinsic traits and extrinsic factors related to climate. The first theme (linking survival, environment, and life history traits) integrates perspectives on trade-offs between survival, body size and reproduction, and between survival, body size, and energy metabolism across two different climatic gradients: latitude and elevation, respectively. The second theme (developing tools to better estimate survival) focuses on stage-specific differences in survival estimates, and describes a method for assigning individuals to age classes in order to refine survival rate estimates of adult versus juvenile birds.

1.3.1 Linking survival, environment, and life history traits

My thesis addresses the long-held view that tropical birds are longer lived than temperate species. This view is rooted in the fact that avian clutch size declines with latitude (Moreau 1944, Lack 1947, Skutch. 1949), an observation that has led to the reasoning that tropical species should offset a reduced clutch size by having higher adult survival (Murray 1985). Although this survival–reproduction trade-off is predicted under LHT, few empirical works have focused on the relationship between latitude and survival. This is partly due to the difficult nature of estimating survival, which requires initial capture and subsequent recapture, resighting, or

recovery of marked individuals (Sandercock 2006). Those studies which have examined variation in survival and latitude are northern-hemisphere biased or focus on only a narrow group of taxa (Peach et al. 2001, Lloyd et al. 2014, Muñoz et al. 2018). Failure to include data from tropical and austral regions, where the majority of species occur, represents a major drawback in our in our ability to generalize relationships between survival and latitude to the diverse life history of birds found worldwide (Martin 2004). To overcome this challenge, I synthesized data in Chapter 2 on over 1,000 estimates from nearly 250 studies of avian survival around the globe. *The main objective of this chapter was to confirm the existence of a latitudinal survival gradient and test the relative importance of climate and key life history traits in predicting these patterns.* By applying a meta-analytical framework, I was able to examine interactions between intrinsic traits and lineage-specific effects as well as the underlying extrinsic climatic factors that may explain global patterns of avian survival. Critically, unlike other studies which have tested the latitudinal survival gradient, I calculate regression lines of survival for the northern and southern hemispheres separately. Doing so better reflects the variation in climatic variables that underlie the latitudinal gradient in the first place.

A proximate mechanism proposed to explain the tropical-temperate survival relationship is that the lower metabolic rates of tropical species reduce intracellular damage, delaying mortality (Daan et al. 1990, Williams et al. 2010, Vágási et al. 2019). However, tropical regions harbor strong environmental gradients of their own, and it remains to be shown whether similar life history trade-offs between metabolism and longevity are reflected among tropical birds of the same latitude. Moreover, tropical mountain ranges provide a natural control for clutch size because most tropical passerines lay only two eggs compared to the much greater variation in clutch size observed across latitudes (Jetz et al. 2008b) and over temperate mountain ranges

(Hille and Cooper 2015, Boyle et al. 2016). In Chapter 3, I explore the energy-metabolism-survival relationship by utilizing data on basal metabolic rate (BMR) and survival rates estimated from the same population of tropical birds in southeastern Peru. Despite the widely held belief that metabolic rate plays a central role in constraining the evolution of survival rates, and ultimately, lifespan, there is scant empirical evidence to support this idea. *My main objective in this chapter was to determine whether BMR, elevation, or both, predicted survival across tropical forest bird species.* To control for the confounding effects of increasing elevation and, hence, increasing thermoregulatory costs due to lower temperatures, potentially elevating BMR, I used phylogenetic path analysis to model effects of elevation on both BMR and survival, as well as accounting for species phylogeny and body size.

1.3.2 Developing tools to better estimate survival rates

Moving from examining ultimate and proximate causes of variation in survival rates, in Chapter 4 I address the extent to which Neotropical birds can be aged in the hand. I accomplished this by studying an often-over-looked aspect of avian life history, the annual renewal of body and flight feathers, or molt. In addition to its general importance to the avian life cycle, an understanding of molt patterns and their resulting plumages can facilitate age classification, thereby providing a useful conservation tool to account for stage-specific differences in survival rates between adults and juveniles. This is done by the identification of multiple generations of feathers, known as molt limits, within the wing coverts and flight feathers (Mulvihill 1993, Jenni and Winkler 1994, Pyle 1997a, 1997b). These methods are well developed in North America and Europe, but remain undescribed for the majority of species elsewhere (Ryder and Wolfe 2009, Wolfe and Pyle 2012, Rueda-Hernández et al. 2018).

Although the advent of age-based approaches to modeling avian survival are not new (Lebreton et al. 1992), the majority of studies treat age classes as ecologically equivalent for two main reasons. First, estimating stage-specific survival requires data to be partitioned by groups, decreasing overall effective sample size for any one group. Many researchers are therefore reluctant, or unable to investigate age-related effects on survival. Second, because differences in the appearance and / or measurements of adults versus juveniles are often unknown, particularly for tropical species, researchers may simply be unable to distinguish between age-classes. *The main objective of Chapter 4 addresses this latter issue by synthesizing data on the number of South American passerines with information on molt limits, which can be used for age categorization. The second objective of this chapter was to develop aging and sexing techniques for one of the most commonly studied groups of tropical birds: manakins.* If molt limits can reliably be used to age tropical birds, then this would provide an important development in understanding avian life-history evolution.

1.3.3 Conclusions

Finally, in Chapter 5 I summarize the main findings from each of the above chapters, highlighting the need for increased long-term monitoring of tropical populations and studies that account for stage-specific variation in survival rates. I assess the limitations of my studies and offer recommendations for future research directions. *My main objective here is to provide a synthetic appraisal of the factors influencing survival rates in tropical birds and how these might be impacted under future of climate warming.*

1.4 Summary

In this dissertation, I use a combination of theory, comparative approaches, correlative field observations and natural history to link survival rates to intrinsic life-history traits and extrinsic climate factors. My work explores both proximate and ultimate causes of variation in survival rates to test critical predictions generated by LHT. Additionally, I provide previously undescribed accounts of age criteria for commonly studied species of Neotropical manakins, which can be applied in mark-recapture analysis to improve our understanding of stage-specific variation in survival rates. This dissertation therefore advances our collective knowledge on life history theory in general, and life history trade-offs and constraints of survival rates in tropical birds, specifically. My work addresses the following questions related to the life history correlates of survival.

1. Does survival increase with decreasing latitude?
2. Is there an inverse relationship between basal metabolic rate and survival?
3. To what extent can molt limits be used to age Neotropical birds?

Chapter 2: A meta-analysis of global avian survival across species and latitude

2.1 Introduction

Aves, a class represented by around 10,000 species, display a broad diversity of morphologies and behaviors, and also show considerable variation in their lifespan and annual survival. For example, in large-bodied landbirds, such as some raptors and parrots, annual survival is often high (Newton et al. 2016, Maestri et al. 2017) and individuals are long lived, but for small-bodied species like warblers and kinglets, rates of annual survival can be low (DeSante et al. 2015, Johnston et al. 2016). While differences in body mass account for some of this variation — larger species tend to live longer than smaller ones (Lindstedt and Calder 1976, 1981, Promislow 1993, Speakman 2005) — many species live longer or shorter lives than predicted given their body mass (Healy et al. 2014). Other aspects of life history, particularly the demographic cost of reproduction, may explain this residual variation in survival rates (Williams 1966, Stearns 1992, Roff 2002). This view stems from the hypothesis that limited resources (i.e., time and / or energy) result in an allocation trade-off between two competing vital functions; specifically, current reproduction reduces future reproduction and survival. The pivotal survival–reproduction trade-off has been well documented in birds (Ricklefs 1977, 2000, Saether 1988, Linden and Møller 1989, Martin 1995b, Ghalambor and Martin 2001), and with the observations of early investigators that the number of eggs laid declines from the poles towards the equator (Moreau 1944, Lack 1947, Skutch. 1949), it has given rise to the expectation that tropical species should offset a reduced clutch size by having higher adult survival (Murray 1985).

There are many studies that suggest high adult survival in tropical birds, the majority of which focus on comparisons between north-temperate systems and the tropics (Martin 2004).

Early reports of high survival came from studies equating survival estimates with return rates, the proportion of individuals marked in one year of sampling and recaptured the following year (Snow 1962, Fogden 1972, Fry 1980, Bell 1982, Dowsett 1985). While these studies deepened our understanding of life-history strategies in tropical birds, estimates based on return rates are problematic because they confound estimation of complicated functions of survival rate and capture probability (Nichols and Pollock 1983, Krementz et al. 1989, Sandercock 2006). More recently, studies employing improved methods for estimating survival via Jolly-Seber (JS) and Cormack-Jolly-Seber (CJS) models, which separate apparent survival (i.e., Φ : the product of true survival and site fidelity) from encounter probability (Sandercock 2006), have reinforced the idea of higher adult survival at lower latitudes (Faaborg and Arendt 1995, Johnston et al. 1997, Francis et al. 1999, Peach et al. 2001, McGregor et al. 2007). The generality of these findings, however, has been questioned based on comparisons showing negligible differences in survival between Central and North American birds (Karr et al. 1990), and lower than expected survival rates for birds from South America (Blake and Loiselle 2008). Other studies have even found higher survival rates for south temperate birds compared to tropical species in Africa (Lloyd et al. 2014). Only one quantitative review has formally addressed latitudinal patterns in adult survival rates of birds across a broad range of latitudes. Muñoz *et al.* (2018) showed that adult survival was higher for species in the tropics compared to those in five sites across the north temperate zone, supporting the hypothesis of a latitudinal gradient in survival, at least for forest-dwelling passerines in the western hemisphere. Yet, despite longstanding interest in the idea of a latitudinal gradient in survival, we still lack an empirical synthesis at the global scale, which stands as a limiting factor in our ability to generalize these relationships to the diverse life history of birds found worldwide (Martin 2004).

Most explanations for a latitudinal survival gradient are based on the assumption of consistent latitudinal variation in survival and other life history traits with which it covaries, such as clutch size (Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997, Peach et al. 2001, McGregor et al. 2007). Indeed, most comparative studies of variation in life history traits treat northern and southern latitudes equivalently (Jetz et al. 2008b, Muñoz et al. 2018, Terrill 2018). However, this assumption may not always be met, since latitude itself does not directly influence organisms per se; rather, environmental factors that covary with latitude exert selective pressures on life history traits. For example, although there exists a global latitudinal gradient in clutch size (Cardillo 2002, Jetz et al. 2008b), this trend is dampened in the southern hemisphere — south temperate species lay smaller clutches than those in the north temperate hemisphere (Yom-Tov et al. 1994, Martin 1996, Evans et al. 2005). Consistent with this pattern, south temperate birds in Africa also tend to be longer lived than their north temperate European counterparts (Lloyd et al. 2014). This hemispheric asymmetry may in part be due to differing climatic conditions between northern latitudes and equivalent southern ones. Namely, south temperate latitudes are less seasonal and have higher minimum winter temperatures (Chown et al. 2004), both of which have been hypothesized to decrease adult mortality and lead to smaller clutch size (Ricklefs 1980). Similarly, clades and their intrinsic traits that may influence survival rates are also distributed nonrandomly across environmental gradients (Jetz et al. 2008b, Sibly et al. 2012). Migratory habit, for instance, arises at least in part from species occupying higher latitudes and experiencing seasonal environments with lower minimum winter temperatures, and there can be substantial deleterious effects on survival over the migratory phase of the annual cycle (Sillett and Holmes 2002, Rockwell et al. 2017). Thus, the geographic variation in survival rates reflects a composite of extrinsic factors, intrinsic traits, and historical events related to the

lineage of a species.

Because previous analyses of the latitudinal gradient in survival have focused on the north-temperate / tropical model (Martin 2004, Muñoz et al. 2018) and have relied on a relatively narrow group of taxa, our current perspective of the biological underpinnings of the geographic variation in survival rates remains somewhat limited. Here, we present data on survival rates for 681 species of landbirds gathered from around the world (Figure 2.1). The purpose of our analysis was to test the relative importance of latitude and extrinsic climate factors (temperature, precipitation, and seasonality) in explaining geographic patterns of avian survival rates, and to ask whether including intrinsic traits (body mass, clutch size, migratory habit) improved model predictions. Specifically, we ask: (1) Is there a latitudinal gradient in adult survival and, if so, are there differences between hemispheres? (2) Do climate measurements (extrinsic factors) explain differences in survival rates as well as latitude? (3) Do intrinsic traits explain additional variation in species-level survival rates? We tested for these relationships in both passerines and nonpasserines and between Old World and New World birds from mainland and island populations. By integrating data on macroecological processes with comparative biology, our modeling approach provides a powerful tool for understanding the diversity of life histories that have evolved across the globe.

2.2 Methods

2.2.1 Assembling a global dataset of avian survival rates

We conducted a search of the peer-reviewed literature for studies that measured survival rate in birds, relying primarily on Web of Science Core Collections and Google Scholar. We also included data for survival rates of North American birds downloaded from the Monitoring Avian

Productivity and Survivorship (MAPS) program (DeSante *et al.* 2015). For each study, we extracted information on annual survival rates and their associated standard errors. When the same study provided separate estimates for males and females, or where estimates were made for different time periods, ages of adult birds, or circumstances (e.g., successful breeders vs. unsuccessful, brood parasites present vs. absent) we took the geometric mean of those estimates. When estimates were available from different habitat types within the same study (e.g., logged vs. unlogged forest), we took the geometric mean of those estimates, provided that the study found no significant differences between groups. If group estimates were reported as significantly different, we chose the estimate from the control group for our analysis. A list of the 249 studies included in our analysis is available in Appendix A Supplementary references.

2.2.2 Extracting data for latitude, climate, and species' intrinsic traits

In order to assess the relationship between survival and latitude, we recorded the geographic coordinates for each species in each study from information provided in the paper itself or by locating the study area on Google Maps. For 26 studies that measured survival over broad spatial scales, such as at the national or continental level (e.g., the MAPS dataset; DeSante *et al.* 2015), we calculated the centroid of the breeding range for each species within the area specified by the study with occurrence data extracted from eBird using the *auk* package (Strimas-Mackey *et al.* 2018) in R (v.3.5.3; R Core Team 2019). This allowed us to estimate a unique latitude and longitude for the centroid of a realized breeding range for each species rather than simply selecting an unweighted point in the study area itself. Further details describing our use of program *auk* are available in Appendix A Supplementary methods.

As latitude is often used as a surrogate for variation in climatic conditions between the north and south poles, we evaluated the predictive power of three key extrinsic factors that characterize the environment of a species and are hypothesized to influence avian survival: annual precipitation (Rockwell et al. 2017, Shogren et al. 2019), minimum winter temperature (Robinson et al. 2007, Salewski et al. 2013), and temperature seasonality (Ricklefs 1980, Lloyd et al. 2014). We retrieved all information on climate measurements from WorldClim Global Climate Data averaged over 1970-2000 (Fick and Hijmans 2017) at 2.5-minute spatial resolution. We extracted data for total annual precipitation (*Precip*, mm), minimum temperature of the coldest month (*Temp_{winter}*, °C) and calculated temperature seasonality (*Temp_{seasonality}*, °C) following Jetz et al. (2008) as the difference between mean summer and winter temperatures averaged over 3-month periods.

We also tested whether species' intrinsic traits explained global patterns in avian survival rates by collecting data on body mass, clutch size, and migratory habit. We obtained body mass (measured in grams) from information contained in the paper, or from the "Elton traits" database (Wilman et al. 2014), or Handbook of birds of the World Alive (del, Hoyo et al. 2019). Similarly, we extracted data on clutch size when it was presented in the paper itself and used published standard reference databases (Jetz et al. 2008b, del, Hoyo et al. 2019) when it was not. No data for clutch size was available in either the paper or reference databases for eight species of tropical birds. In these cases, we used clutch size of sister species or other closely related taxa. Following del Hoyo *et al.* (2018), we classified species as either migratory or non-migratory. We considered migratory species to be those that regularly undertook seasonal movements >100 km (i.e., short- and long-distance migrants). While some species do not clearly conform to this

dichotomy, it is useful way to contrast important sources of mortality that could influence survival rates.

2.2.3 Statistical analysis

We used logit survival as the response variable in our models to account for nonlinear associations with extrinsic and intrinsic predictors. Prior to analysis, we \log_{10} transformed body mass and clutch size due to skewness, and scaled latitude and climate data to z scores by subtracting their mean and dividing by their standard deviation. Most variables were weakly correlated, although both measures of temperature reached Spearman rank correlations >0.75 (Table A.1). To estimate adult survival rates along the latitudinal gradient, we used a multi-level meta-analytical framework using the R package *metafor* (Viechtbauer 2010), which fits random and fixed effects models, weighting effect sizes by the inverse of their squared standard error. For each model developed, we accounted for sources of non-independence in our dataset that can arise when multiple survival estimates are extracted from the same study, are available for the same species, and / or due to common ancestry, by fitting study identity, species identity, and phylogeny as random intercepts. To incorporate phylogeny, we used a majority rules consensus tree derived from a set of 1,000 randomly-selected trees based on the global phylogeny of birds (Jetz et al. 2012), and pruned to our study taxa (Figure A.1) with the R package *phytools* (Revell 2012). We used the branch length from this consensus tree to specify values for the model variance-covariance matrix.

We first ran a random effects only model on the entire dataset using the *rma.mv* function to estimate a pooled effect size of global avian survival rates. Given potential differences in selection pressures experienced by passerines vs. nonpasserines, species from Old World

(Afrotropics, Indomalayan, Palearctic) vs. New World (Neotropics, Nearctic) biogeographic realms, and mainland vs. island bird populations, we also evaluated separate meta-analytic models using effect sizes for these six data subsets. We considered point estimates to be different from one another if their 95% confidence intervals (CI) did not overlap. We quantified total heterogeneity of each dataset by calculating Cochran's Q and I^2 statistics (Higgins and Thompson 2002).

To test for publication bias in our global dataset we used three complimentary methods: (1) We visually assessed asymmetry of funnel plots (Figure A.2); they appeared close to symmetrical. (2) We removed studies that reported survival estimates for >10 species, and which accounted for 64% of effect sizes, and reran the analysis. We repeated this procedure for studies conducted for <10 years to examine the effects of study duration on survival estimates. (3) We fit additional models where study method (i.e., live-recapture, dead recovery, or both) was used as an explanatory variable or whether package *auk* was used to calculate the geographic coordinates. Results of this sensitivity analysis were all qualitatively similar to the global mean survival rate based on the entire dataset (Figure A.3).

We conducted meta-regressions (meta-analyses incorporating explanatory variables, hereafter referred to as “moderators”) whereby we determined the effects on species-specific adult survival rates of (1) latitude, (2) extrinsic climatic factors, and (3) intrinsic traits in accordance with hypotheses described from the primary literature. We began by comparing fit of a latitude-only model, where regression slopes varied between hemispheres, to single-predictor linear models testing the influence of moderators on adult survival rates (Table A.2). We next used AIC_C values (Burnham & Anderson 2002) to guide selection of a multi-predictor model of extrinsic climatic factors and intrinsic traits separately. Starting with the moderator that had the

lowest AIC_C value, we sequentially added the next strongest moderator until AIC_C was no longer improved (Table A.3). We considered the model that minimized AIC_C the most appropriate if it had fewer parameters and was at least 2 AIC_C less than the next most competitive model (Arnold 2010). All of the intrinsic moderators we assessed improved model fit and were carried forward to the next step of model development. Temperature seasonality (*Temp*_{Seasonality}) provided the best model fit for extrinsic moderators. We then combined both sets of moderators into a joint extrinsic / intrinsic model and repeated analysis using the global dataset and each of the six data subsets.

2.3 Results

2.3.1 Meta-analytic means

The global meta-analytic back-transformed mean survival rate of all birds calculated over 1007 effect sizes and representing 681 species and extracted from 249 publications, was 0.68 (95% CI = 0.48 to 0.83; Table A.4). Overall, the joint extrinsic / intrinsic model explained variation in survival well (Figure A.4, adjusted $r^2 = 0.43$). When we estimated separate meta-analytical means for the six data subsets, we found similar values with overlapping 95% confidence intervals between the global mean and mean effect sizes calculated for passerines vs. nonpasserines, Old World vs. New World biogeographic realms, and estimates from mainland vs. island birds (Figure 2.2; Table A.4). In addition, all models had values of $P < 0.0001$ for Q_E and $I^2 > 90\%$, which indicated that substantial heterogeneity remained unexplained among studies and warranted our subsequent step of evaluating moderator variables.

2.3.2 Relationships between intrinsic and extrinsic moderators

We found evidence supporting the hypothesis of a latitudinal gradient in survival, and this effect was most apparent in the northern hemisphere. When we examined model predictions from a single-predictor model of latitude over the entire dataset, the odds of survival decreasing were 1.35 times greater for every 1° increase in latitude in the northern hemisphere compared to the southern hemisphere (Figure 2.3a). Similarly, the global joint model showed a negative, albeit nonsignificant, effect of latitude on survival for northern hemisphere species ($\beta = -0.121$, 95% CI = -0.293 to 0.050), while estimates for those inhabiting the southern hemisphere were close to zero ($\beta = -0.016$, 95% CI = -0.130 to 0.097; Table 2.1, Figure 2.4). Driving this global trend at northern latitudes was a significant negative effect size for passerine birds ($\beta = -0.252$, 95% CI = -0.448 to -0.056; Figure 2.4b) and a marginally significant effect of species / populations from the mainland ($\beta = -0.142$, 95% CI = -0.315 to 0.031; Figure 2.4d). In contrast, effect sizes calculated for southern latitudes were generally smaller, and the overall slope of the meta-regression line of the global model was shallower compared to the northern hemisphere (Figures 2.3a and 2.4). Only New World species (i.e., birds from South America) showed a significant negative association with latitude ($\beta = -0.211$, 95% CI = -0.378 to -0.045; Figure 2.4c). Of the extrinsic climate moderators we considered, temperature seasonality was the most competitive within our AIC model selection framework (Table A.2 and A.3), although only marginally so compared to minimum winter temperature. Regardless of which climate moderator was used in the joint model, the effect calculated over the global dataset and for all data subsets was nonsignificant (Figure 2.4).

In general, the relationship between survival and intrinsic life history traits was stronger than those of either climate or latitude (Figure 2.4; Table 2.1). Effect size estimated from the

global model was positive for mass ($\beta = 0.236$, 95% CI = 0.189 to 0.284; Figure 2.3c) and negative for clutch size ($\beta = -0.507$, 95% CI = -0.641 to -0.373; Figure 2.3d), which means that avian survival was higher for larger birds and for those with smaller clutch sizes. With the exception of mass for island species, similar results for both moderators were found for all data subsets (Figure 2.4). When we included nonmigrant as a moderator in the global model, the effect size was small and positive, with confidence intervals marginally overlapping zero ($\beta = 0.016$, 95% CI = -0.005 to 0.039; Figure 2.4), suggesting higher survival for year-round residents. This effect was strongest for passerines ($\beta = 0.147$, 95% CI = 0.011 to 0.254; Figure 2.4b) and Old World birds ($\beta = 0.237$, 95% CI = 0.062 to 0.412; Figure 2.4c).

2.4 Discussion

2.4.1 Global-scale patterns of avian survival with latitude

We found support for the oft-touted latitudinal survival gradient, but this depended on both the geographic region and taxa being considered. Specifically, we demonstrate that the previously noted inverse relationship between latitude and survival is only weakly borne out across northern hemisphere avifauna overall, but that this effect is strengthened when considering only passerines or species inhabiting the mainland. In contrast, the relationship was only evident in the southern hemisphere for survival estimates from New World birds, the vast majority of which were passerines. When considered independently, there was no indication that nonpasserines had higher survival with decreasing latitude in either hemisphere. Overall, our meta-analysis reveals that while some tropical birds may live longer than their temperate counterparts, the shape of the latitude-survival response is likely to differ among species and between hemispheres.

Our synthesis is the first to assess global-scale patterns in avian survival rates; previous studies have either been limited geographically (Karr et al. 1990, Peach et al. 2001, Lloyd et al. 2014), or have focused on a narrower range of species, such as raptors (Newton et al. 2016) or shorebirds (Méndez et al. 2018). To date, the most extensive analysis of avian survival and latitude comes from a study of 12 locations spanning 60° across the Americas (Muñoz et al. 2018). Our global-scale analysis compliments that of Muñoz *et al.* (2018), who reported a linear decrease in survival of roughly 2.1% for every 10° increase in latitude for passerine birds from Alaska to Peru, similar to what we observed for northern hemisphere species worldwide. While both our studies used a meta-analytical approach, Muñoz *et al.* (2018) conducted their analysis using a Bayesian mode of inference and considered only forest-dwelling passerines, while our study includes survival estimates of both passerines and nonpasserines from a variety of habitats, which we investigated using a maximum-likelihood approach. We also fit regression lines for latitude both north and south of the equator rather than testing the relationship between survival and absolute latitude. This latter point is particularly important, given that one general explanation for spatial patterns in life-history traits is that they arise from natural selection imposed by latitudinal gradients in environmental conditions (Cardillo 2002), which differ between hemispheres (Chown et al. 2004). Despite our use of different methods, the fact that we obtained some common results lends increased support to the overall relationship. Moreover, with our analysis, we provide a strong mechanistic basis for understanding variation in survival rates, as it better reflects the climatic variables that underlie latitude in the northern and southern hemispheres.

Hemispheric asymmetries in other patterns of avian life-history traits, such as timing of reproduction (Covas et al. 1999), clutch size (Moreau 1944, Martin et al. 2006, Lloyd et al.

2014), and parental care (Russell et al. 2004, Llambías et al. 2015), are well documented. The global patterns we identified are also congruent with the idea of a differential response of life-histories between hemispheres — we detected an inverse relationship between survival and latitude in the northern hemisphere but found little indication that this association was mirrored by southern hemisphere species overall. Only when we analyzed biogeographic realms in the southern hemisphere separately did we find that New World birds showed higher survival with decreasing latitude. This pattern is deceptive, however, since southern hemisphere nonpasserines account for little more than 1% of the effect sizes analyzed in the New World data subset. We therefore interpret this result as evidence of the latitudinal survival gradient in South American passerines. This means that for Old World birds, tropical species had similar survival rates to birds from the austral zone, and this was likely to be true regardless of whether they were passerines or nonpasserines. Survival estimates from Australasia and Oceania, biogeographic realms not traditionally included in the New / Old world classification, also reflected this same pattern and showed no evidence of a negative relationship with latitude.

Such differences may be explained, in part, by the historical geography and latitudinal positions of the continents. For the last 15 million years, South America has extended roughly 20° further into the southern hemisphere than continental landmasses in the Old World. Thus, one reason we may have detected a negative trend in survival for southern hemisphere birds, but only in the New World, could simply be due to the greater range of latitudes and climatic conditions available to landbirds from South America with which to adapt. For example, latitudes greater than 35° S are characterized by higher seasonality and mean annual temperatures $\leq 0^{\circ}\text{C}$ (Chown et al. 2004); thus, this result may be indicative of a threshold response of avian survival to freezing temperatures and / or a more seasonal environment.

Supporting this idea, mean survival of South American passerines that occurred at latitudes higher than 35° S (survival rate = 0.38, n = 8) was lower on average than those from the highest latitudes occupied by birds in Africa (Old World survival at 34° S = 0.69, n = 19). Only one other study has addressed the question of a latitudinal survival gradient in the southern hemisphere; Lloyd *et al.* (2014) found no indication of higher survival for birds living in tropical Malawi compared to austral South Africa. Our results are congruent with those findings and suggest that higher survival of tropical birds may be a pattern localized primarily to passerines from the northern hemisphere and in South America, where factors such as a more seasonal environment may limit resource availability and constrain species survival.

2.4.2 Influence of Climate on Survival

Our results suggest that temperature seasonality, at least at the resolution that we examined it, is a poor predictor of avian survival. Indeed, latitude-only models out-performed single-predictor models of extrinsic climate factors for each of the moderators we considered by a minimum of $>4.88 \Delta AIC_C$ (Table A.2). Although temperature seasonality was not significant, our finding of higher survival in the southern hemisphere, but only for New World birds, is in accordance with reported asymmetries in climate between hemispheres. Compared to north-temperate latitudes, austral latitudes are characterized as less seasonal in general, having higher minimum winter temperatures and higher, less variable patterns of precipitation (Chown *et al.* 2004). That said, South America does possess environments with climates closer to those of the northern hemisphere (e.g., mean temperatures $\leq 0^\circ\text{C}$, higher temperature seasonality) compared to Africa and Asia, which lack such climate analogs at their southern-most latitudes. Although latitudinal variation in life history traits arises in part from natural selection imposed by complex

interactions among environmental factors, latitude as a ‘catch-all’ variable provided a more complete picture of global variation in survival. For example, temperature seasonality fails to capture the negative latitude-survival relationship in passerines because this effect is counteracted by pooling data for taxa from different regions; specifically, combining data with estimates for southern hemisphere passerines from the Old World. It appears, therefore, that latitude remains one of the best methods to portray the suite of climatic constraints characterizing the environment of a species, but only when northern and southern hemispheres are examined independently.

2.4.3 Intrinsic traits mediate variation in the latitudinal survival gradient

We find that the association between body mass and survival and reproduction and survival — two of the cornerstone trade-offs of life history theory (Stearns 1992) — are well supported by our meta-analysis, suggesting higher survival for larger birds and those with smaller clutch sizes. Notably, when mass and clutch size were included in the joint model, the strength of the latitudinal survival gradient was diminished (Table 2.1). Similarly, we found general support for the idea that sedentary behavior favors higher survival and, hence, shifts towards slower life-histories often associated with tropical latitudes. These results highlight the importance of considering the interplay between intrinsic and extrinsic variables when investigating macroecological processes. Latitude of course is associated with the changes in many aspects of avian life history, including migratory behavior (Alerstam et al. 2003), clutch size (Cardillo 2002, Jetz et al. 2008b) and body mass (Olson et al. 2009), all of which have been demonstrated to increase globally with increasing latitude. Combined with these findings, our results are in accordance with the theory of a slow-fast life-history continuum (Ricklefs and Wikelski 2002)

and suggest that while birds at tropical latitudes tend to be longer lived and have reduced clutches given their body size, this is far from the full picture. Global patterns of avian survival are driven by interactions between intrinsic traits and lineage-specific effects of latitude and their associated climatic factors.

2.4.4 Challenges in evaluating avian survival

Adult survival estimates are affected by several methodological caveats that we consider here. First, a general problem with comparing survival studies is that differences between estimates derived from old versus new methods and between live recaptures and dead recoveries may mask trends in the data (Roodbergen et al. 2012). Our dataset consisted primarily of studies that used live capture-mark-recapture techniques (83% of effect sizes) and most of these were conducted since 2000; nearly all studies were conducted after 1990 when modern statistical tools for analyses of marked animals were developed (Lebreton et al. 1992). One of the drawbacks of capture-mark-recapture data is that the reported metric, apparent survival, is a product of true survival and site fidelity and as such will always be biased low, whereas estimates of survival from dead recovery models are often interpreted as true survival (Sandercock 2006). Biases in survival estimates may therefore be strong for birds from tropical regions, which consisted exclusively of live-recapture data, and where behaviors such as altitudinal migration are more common than in temperate regions (Barçante et al. 2017) and can lead to temporary emigration from study plots. Another issue affecting the comparison of survival studies is the study duration. This, too, may be particularly problematic for tropical regions, where data collection is often hampered by sampling conducted over irregular or insufficiently long intervals to produce robust estimates of survival (Ruiz-Guitérrez et al. 2012). For example, in our meta-analysis 62% and

69% of effect sizes from austral and temperate latitudes, respectively, were calculated from datasets spanning >10 years, compared to only 34% from tropical latitudes. However, in a study of tropical birds comparing survival estimates derived from 6 vs.12 years of data, Blake & Loiselle (2013) reported an improvement in precision, but no change in point estimates for survival. Still, other authors argue that longer time frames are needed to generate reliable survival estimates for tropical resident species (i.e., 10–30 years), given their expected longevity and low recapture probabilities ($p < 0.25$; Ruiz-Guitérrez *et al.* 2012). Despite these problems with the comparability of the data, we found no indication that difference in methodological approaches strongly biased our results (Figure A.3).

2.4.5 Conclusions

Based on a global-scale synthesis of avian survival rates, we find evidence that survival increases with decreasing latitude, but that this phenomenon is more nuanced than previous descriptions have characterized. Specifically, we demonstrate that the latitudinal survival gradient is stronger in northern hemisphere species, where climate seasonality may be greater. By including aspects of species life history traits in our models, we could explain a greater portion of the variation in survival rates than with latitude alone. These results indicate the importance of considering an organism's intrinsic traits as well as the extrinsic factors of their environment when describing broad scale macroecological patterns. Where peaks in survival occur, how they relate to climatic variables, and how these patterns are likely to change through time and space given the effects of climate change, are of major importance for conservation. We hope that in assembling this database and dissecting some of the global patterns in survival across avian groups and hemispheres, we can provide a platform for future work to target underrepresented regions and

taxa and also make a clear path forward to better understanding variation in survival rates, and how it intersects with other life history traits across the world's avifauna.

Table 2.1 Multi-predictor meta-regression models of avian survival based on only extrinsic factors (*Latitude* and *Temp_{Seasonality}* combined) or intrinsic traits (*Mass*, *Clutch size*, and *Nonmigrant*) or a joint model that included both sets of factors and traits. *Latitude* was fitted with separate intercepts for the northern and southern hemispheres, *Temp_{Seasonality}* is the difference in mean temperature of the three warmest vs. three coldest months, and *Nonmigrant* is a binary variable representing species migratory habit. ΔAIC_C columns represent the increase in model AIC_C when a moderator is dropped relative to the fully parameterized model. Model coefficients (β), 95% confidence intervals are shown for the full models. Significant effects are denoted as $p < 0.0001$, ***; $p < 0.01$, **; or $p < 0.05$, *. For comparison, AIC_C for the random effects only model was 1613.66.

Variable	Extrinsic	Intrinsic	Multi-predictor models					Joint model					
	ΔAIC_C	ΔAIC_C	β	95% LCL	95% UCL	z	p	ΔAIC_C	β	95% LCL	95% UCL	z	p
<i>Latitude_{Northern}</i>	6.07		-0.23	-0.41	-0.05	-2.51	*	0.74	-0.12	-0.29	0.05	-1.39	
<i>Latitude_{Southern}</i>			-0.01	-0.14	0.12	-0.16			-0.02	-0.13	0.10	-0.29	
<i>Temp_{Seasonality}</i>	1.12		-0.06	-0.14	0.03	-1.27		-0.72	0.00	-0.09	0.08	-0.07	
<i>Body mass</i>		79.40	0.23	0.18	0.27	9.57	***	82.05	0.24	0.19	0.28	9.69	***
<i>Clutch size</i>		67.53	-0.56	-0.68	-0.44	-8.99	***	46.81	-0.51	-0.64	-0.37	-7.43	***
<i>Nonmigrant</i>		6.69	0.15	0.04	0.25	2.79	**	1.54	0.10	-0.02	0.22	1.69	

Figure 2.1 Location of effect sizes from 249 studies used in the meta-analysis of avian survival rates. The number of survival estimates reported at each location is illustrated by the size of the circle. Dashed line represents the equator while dotted lines at 23.4° N and S indicate the Tropic of Cancer and Capricorn, respectively, and delineate the tropics.

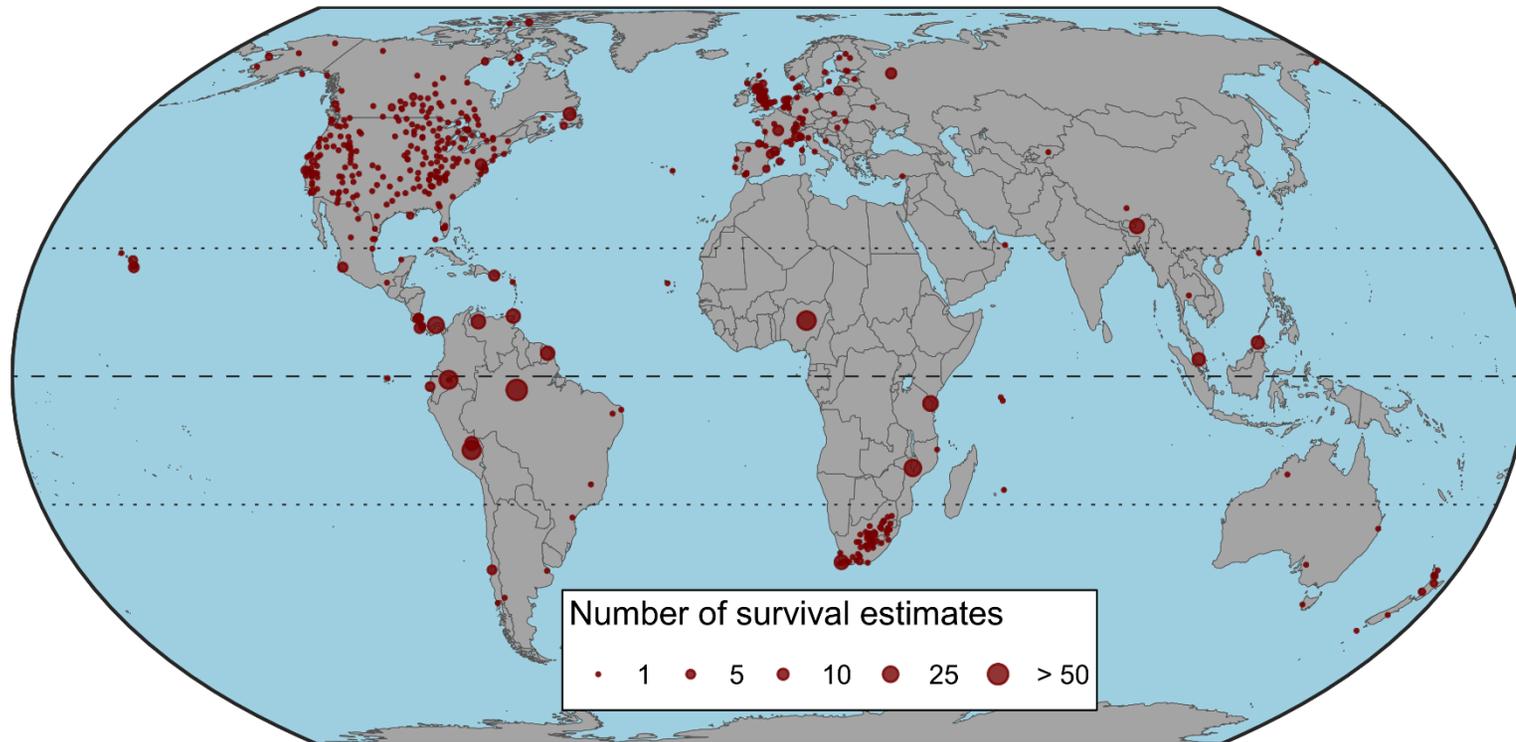


Figure 2.2 Mean avian survival and 95% confidence limits calculated over the entire dataset and from meta-regression models, which estimated intercepts independently for data from passerines vs. nonpasserine birds, Old World vs. New World biogeographic realms, and mainland vs. islands. Number of effect sizes used in each data subset is shown in parentheses. Dashed line indicates the difference from the overall meta-analytical mean (0.68).

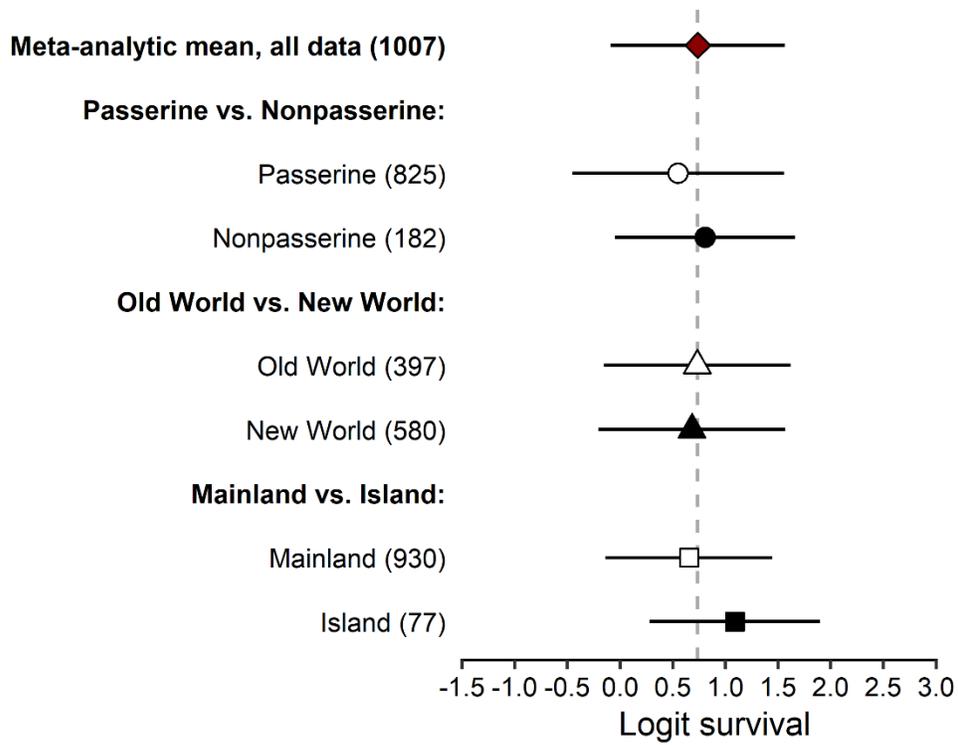


Figure 2.3 Relationship between adult survival rate of birds from the entire dataset and moderator variables included in the joint extrinsic / intrinsic model (Table 2.1). Dashed lines represent the best linear fit based on model predictions estimated from single-predictor meta-regression models in *metafor* with 95% confidence intervals plotted as solid lines. Point sizes reflect the inverse of the standard error used to weight data points (i.e., more precise estimates appear as larger points).

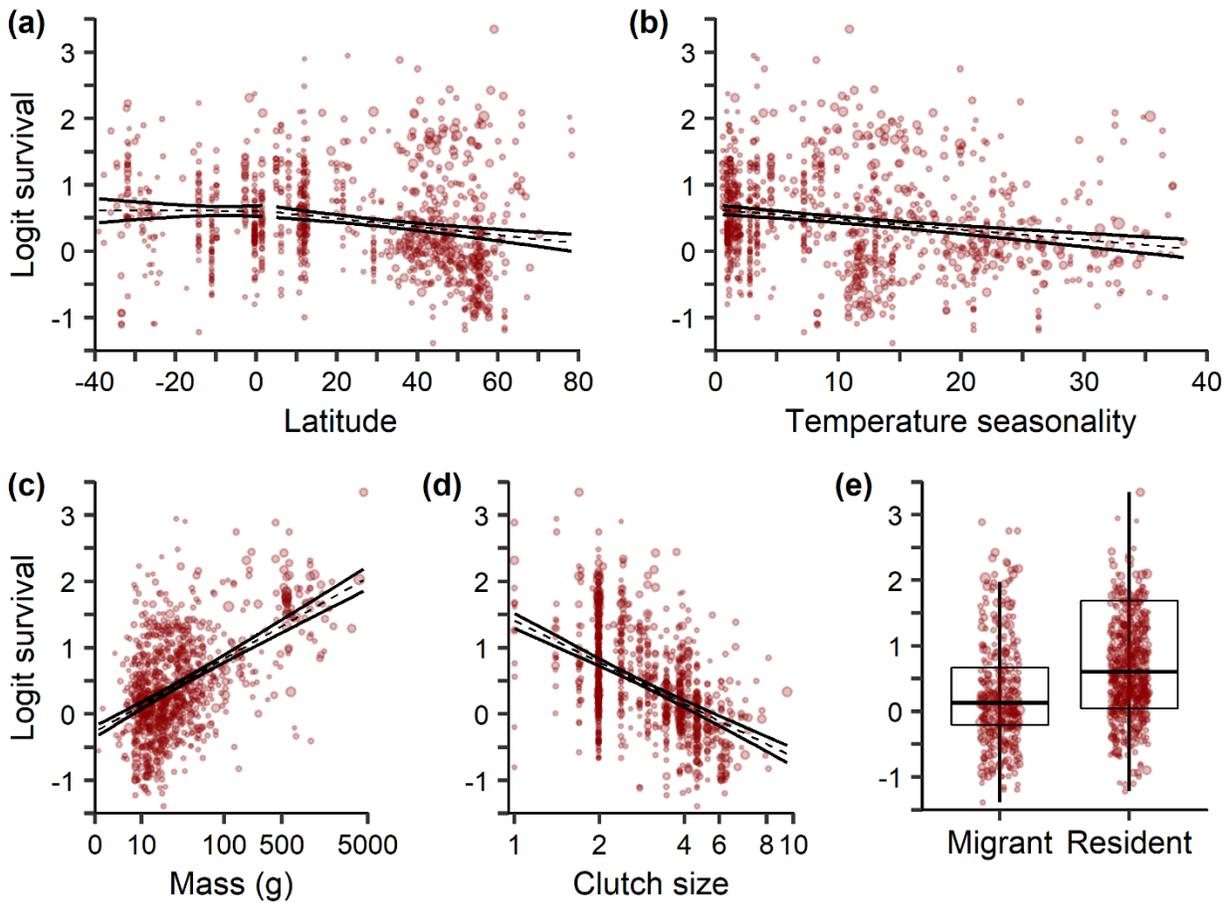
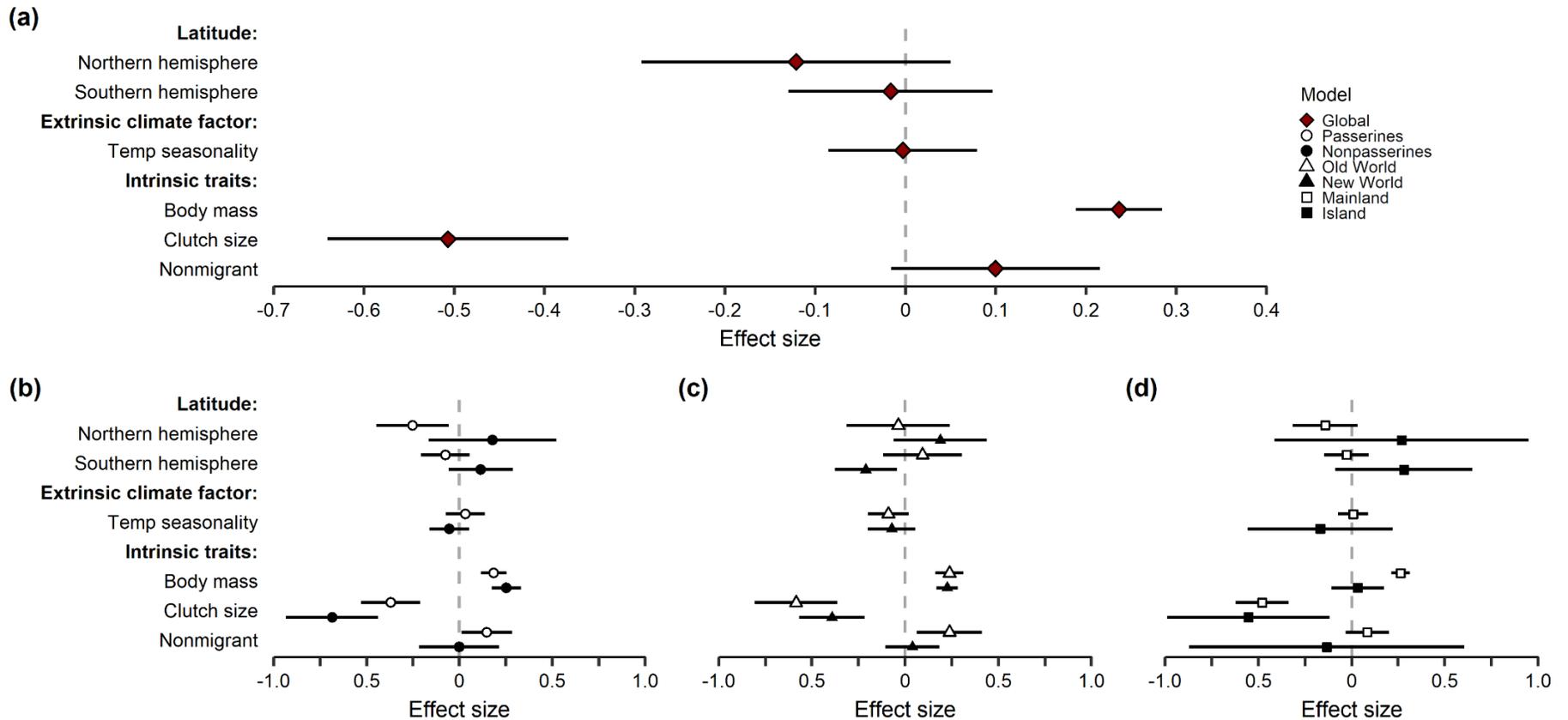


Figure 2.4 Overall effect size estimates for the studies of adult survival based on the joint extrinsic / intrinsic model for the global dataset (a) and over data subsets for passerines and nonpasserines (b), Old and New World birds (c), and species from mainland and island habitats (d). Bars indicate 95% confidence limits. Effect sizes are considered significant where confidence limits do not overlap zero (dashed line).



Chapter 3: Survival is negatively related to basal metabolic rate in tropical Andean birds

3.1 Introduction

Life history strategies are thought to optimize fitness given constraints on species' physiology and ecology (Stearns 1992, Roff 2002) and can be viewed as occurring along a slow-fast continuum (Stearns 1983). According to this view, finite resources impose an allocation trade-off between current versus future reproduction or survival — time and/or energy invested in current reproduction is made unavailable for other purposes. 'Slow' species are characterized as investing less in reproduction, but more in self-maintenance, increasing survival overall; whereas 'fast' species display opposite patterns. These life history strategies are coupled to sets of physiological traits, including metabolic, immunological, and hormonal, that have coevolved in response to ecological conditions to form a 'pace-of-life' syndrome (Ricklefs and Wikelski 2002). Birds have proved useful to 'pace-of-life' studies because they are well-sampled globally and have life history and physiological traits that vary predictably over temperate to tropical latitudes. For example, tropical species lay smaller clutches (Lack 1947, Kulesza 1990, Jetz et al. 2008b), have higher survival (Peach et al. 2001, Muñoz et al. 2018), and display lower basal metabolic rates (e.g. BMR) than north temperate species of similar body mass (Wiersma et al. 2007b, Londoño et al. 2015, Bushuev et al. 2017). Because BMR provides an integrated view of the maintenance energy requirements of an individual associated with its ecological conditions (Daan et al. 1990), it is one of the most widespread and useful measures in linking the flux of energy through an animal with key aspects of their life history (Wiersma et al. 2007a), such as survival.

Attempts to link energy metabolism to survival date to the early 20th century, when Pearl (1928) advanced ‘rate-of-living theory’, a tenet of which is that species with lower metabolic rates live longer. Harman (1956) theorized further that long lifespans are achieved at lower metabolic rates due to reductions in reactive oxygen species (ROS) and the damage they do to cells as a byproduct of aerobic respiration (e.g., Selman, Blount, Nussey, & Speakman, 2012; Speakman, 2005; Vágási et al., 2019). As a result, evolutionary ecologists and physiologists often assume negative correlations between metabolic rate and survival (Speakman et al. 2015), even though relationships between energy metabolism, oxidative stress, and survival are complex and also affected by antioxidant defense and cellular repair pathways (Speakman 2005, Vágási et al. 2019). Moreover, individual BMR can be highly flexible in some species and varies to accommodate seasonal changes in temperature, breeding, or as part of the migratory cycle (McKechnie 2008). Thus, while the over-arching prediction of a negative relationship between avian BMR and survival are strongly supported by patterns in latitudinal gradients (Ricklefs & Wikelski, 2002, Williams et al., 2010), considerable uncertainty surrounds this relationship, and few empirical studies have compared metabolic rate and survival across multiple species at a single site (but see Williams et al. 2010).

Negative correlations of survival, BMR, and latitude suggest that similar trade-offs in life history traits should also be expected across other environmental gradients, such as elevation (Hille and Cooper 2015, Boyle et al. 2016). Birds in particular have developed physiological machinery that has allowed them to adapt and thrive at high elevations more so than any other group of endotherms, including a greater capacity to tolerate and exercise in hypoxia (Scott et al. 2011). High elevation populations of birds in both temperate and tropical regions must deal with decreased partial pressure of oxygen as well as colder temperatures relative to adjacent

lowland/low-latitude species and larger daily fluctuations in temperature, the latter of which can both reduce food availability and challenge individual physiology (Kwit et al. 2004). We might therefore expect the ‘pace-of-life’ syndrome of birds living in high elevation environments to reflect increased rates of energy expenditure due to higher maintenance costs and acclimatization to colder temperatures (McKechnie and Swanson 2010). For instance, populations of White-crowned Sparrows (*Zonotrichia leucophrys*; Weathers et al. 2002) in temperate North America, and Amethyst Sunbirds (*Chalcomitra amethystina*; Lindsay, Downs, & Brown, 2009) and Fiscal Shrikes (*Lanius collaris*; Soobramoney, Downs, & Adams, 2003) in austral Africa all display increased BMR at high elevation. Thus, if high BMR characterizes high-elevation populations, then we might also expect them to exhibit low survival. However, in contrast to temperate regions, data from the tropical Andes failed to find an effect of elevation on metabolism when examining >250 species from Peru across a 2.6 km elevational gradient (Londoño et al. 2015). This result implies that low BMR in tropical birds is unrelated to ambient temperature, changes in oxygen partial pressure, or is offset by the costs of metabolic heat production and reduced thermal conductance at high elevations (Londoño et al. 2017). Links between survival and elevation do receive support from several intraspecific studies of birds at temperate and Holarctic latitudes, with most reporting higher survival in populations at higher elevation (Boyle et al. 2016). High elevation sites in tropical regions differ from the temperate zone in important ways — they are less seasonal and lack the productivity pulses experienced at higher latitudes — so it remains unclear whether populations of tropical mountaintop birds also display higher survival relative to lowland species.

We examined relationships among survival, BMR, and elevation in tropical birds from southeastern Peru to test whether 1) BMR and survival are negatively related, and 2) survival

rates differ between birds living at low versus high elevation. First, we estimated apparent annual survival in 37 Passerine species along an Amazon-to-Andes elevational gradient (400–3000 m) using multi-year mark-recapture data. We then asked whether BMR (previously measured at the same study sites; Londoño et al. 2015), elevation or both predicted apparent survival. Second, we asked if the relationship between BMR and apparent survival was mediated through elevation whereby lower temperatures at higher elevations led to an increase in BMR and subsequent reduction in survival. To disentangle direct and indirect effects of physiology and environment, we used a path analysis while controlling for non-independence of species due to their common ancestry (Felsenstein 1985) and positive allometric effects of body mass on BMR (McNab 2009, Williams et al. 2010, Londoño et al. 2015) and survival (McCarthy et al. 2008). These data represent the first test of elevation, representing an important environmental gradient within the tropics, and BMR, long believed to be negatively related to longevity, to explain variation in apparent survival for tropical birds.

3.2 Methods

3.2.1 Study sites

We conducted our study at three research stations in the Manu Biosphere Reserve, Peru, at 400–3000 m elevation and oriented along a 70 km-long northeast–southwest axis (Figure 3.1).

Pantiacolla is located at the base of the Andean foothills in humid lowland rainforest (12° 38' 31.3" S, 71° 14' 21.2" W). San Pedro includes both humid montane rainforest and lower-elevation cloud forest (13° 3' 19.4" S, 71° 32' 48.5" W). Wayqecha is at the upper boundary of Andean cloud forest near tree line (13° 11' 14.4" S, 71° 35' 9.3" W). A rainy season occurs from November through March with highest rainfall generally in January and February, while May

through July form the dry season (Rapp and Silman 2012). Mean annual rainfall is highest at mid elevations (>4500 mm) while both low and high elevations stations average >3000 mm yr⁻¹ (Rapp and Silman 2012). Annual mean temperature ranges from a low of 11.2 °C at Wayqecha to 23.2 °C at Pantiacolla (Londoño et al. 2015) with a difference of <4 °C between the warmest and coolest months (Rapp and Silman 2012).

3.2.2 Mark-recapture and mist-netting

At each research station, we surveyed for birds at 10 plots in continuous forested habitat using mist-nets (12 x 3 m, 36-mm mesh). Plots were typically positioned adjacent to one another along trails and spanned elevational ranges between 385–575 m at Pantiacolla, 1250–1720 m at San Pedro, and 2515–2985 m at Wayqecha. Each plot covered an area of approximately 1–1.5 ha and consisted of a linear array of 10–15 nets set at ground level placed 5–50 m apart at the same location each year. We timed data collection to overlap with the end of the dry season (August–November), which is also the breeding period for most birds in the region (Londoño et al. 2015). We visited plots for 3 consecutive days and checked nets regularly from ~0600–1600 h. During 2012–2015, a repeat 3-day visit was made to each plot 7–14 days after initial sampling for a total of six days of mist-net surveys per plot. Each plot was surveyed for six years at Pantiacolla and San Pedro, and five years at Wayqecha, where mist-netting began in 2012. Sampling effort varied somewhat among years but was relatively equal across stations overall (Table B.1).

All birds captured were banded with a uniquely marked aluminum leg band (National Band and Tag, Newport, United States). We recorded wing chord, tail length, bill width and length (in mm), and mass for all birds (± 0.05 g, FlipScale F2, www.myweigh.com). Sex and reproductive status were determined by brood patch, cloacal protuberance, or dichromatic

plumage. We aged birds using a combination of plumage characteristics, skull ossification and the extent of body and flight feather molt (Kennedy et al. 2018).

3.2.3 Basal metabolic rate, elevational range, and body mass

BMR was estimated as the mean per species at each of the three field stations as part of a study of energy metabolism in tropical birds (Londoño et al., 2015; Appendix B Supplementary methods). Similar to Pollock, Brawn, Agin, & Cheviron (2019), who found tropical birds exhibited more modest seasonal acclimatization compared with their temperate counterparts, we found little evidence of seasonal variation in BMR and thus did not include sampling date as a potential nuisance parameter in our analysis (Table B.2; Figures B.1 and B.2). We calculated the mean of each species' elevational range based on capture locations within stations. Because our coverage of the elevational gradient was not complete, and also due to the high species turnover with elevation in the study area (Jankowski et al. 2013b), few species were captured at multiple stations and no species was captured in sufficient numbers to model survival at more than one station. We calculated body mass as the mean mass of each species based on capture data.

3.2.4 Estimating adult survival

We used 5531 capture records (1732 recaptures of 3799 individuals) of 37 Passerine species to estimate apparent annual survival (minimum number of captures = 34; mean ratio of captures/recaptures = 2.34, SD = 1.26). Because we were interested in adult survival, we excluded data from 35 cases when we captured birds determined to have recently fledged. For each individual, we created a capture history of their initial capture and subsequent recaptures to model apparent annual survival — the product of true survival and site fidelity — using

Cormack-Jolly-Seber (CJS) models with time intervals adjusted to fractional years to reflect unequal sampling (Table B.3). All mark-recapture analyses and goodness-of-fit (GOF) testing were carried out using *RMark* (Laake 2013) in *R* environment 3.4.0 (R Core Team 2017).

We fitted four *a priori* models that varied in their assumptions of apparent survival (ϕ) and capture probability (p) to each of the 37 species (Table B.4). To estimate ϕ , we considered time-constant (.) and time-since-marking (TSM) models, the latter of which accounts for underestimation of survival due to transient individuals moving through the study area (Johnston et al. 1997). We used TSM models because the proportion of transients in populations of tropical birds are known to be high (e.g., >40% for birds in Panama; Brawn, Karr, Nichols, & Robinson, 1999), especially for frugivorous species, such as tanagers, manakins, and some flycatchers (Martin and Karr 1986). The TSM model allows apparent survival to differ for birds during their first interval after capture (ϕ^1) from survival in the second (ϕ^{2+}) and subsequent intervals. Because ϕ^{2+} is a less-biased estimate of true survival whenever $\phi^1 < \phi^{2+}$ (Sandercock 2006), we did not use estimates of survival from the first time interval (ϕ^1) in our analysis. Due to differences in capture effort among years (Table B.1), we considered models where capture probability varied or remained constant (Table B.4).

To assess model fit, we quantified overdispersion by calculating a variance inflation factor (\hat{c}) obtained by dividing the deviance of each species' most general model by the deviance estimated from 1000 parametric bootstrap simulations. We used the resulting \hat{c} to adjust corrected Akaike information criterion (AIC_C) values to their quasi-likelihood analogue ($QAIC_C$). We considered the model with the lowest $QAIC_C$ the most appropriate model if it had fewer parameters and was at least 2 $QAIC_C$ less than the next most competitive model (Burnham and Anderson 2002, Arnold 2010). Models assuming constant survival and recapture

probabilities had the most support (Table B.4), and for the majority of species there was more than one top model within 2 QAIC_C of the lowest value (Table B.5). When models were within 2 QAIC_C, we used a likelihood-ratio test for all nested sub-models to assess whether the additional parameter significantly improved model fit.

3.2.5 Statistical analysis

We used a multi-step approach to model relationships between BMR, elevation and survival. First, to account for potential nonlinear relationships between elevation and dependent variables, we compared model fit where elevation was continuous (mean capture elevation), categorical (Pantiacolla, San Pedro, Wayqecha), or binary (lowland <1000 m, versus montane >1000 m). Model fit was best for the binary structure (Table B.6) and was carried forward to the next stage of model development that considered the simultaneous effects of all variables within a multivariate framework.

An additional complicating factor when modeling interspecific species relationships is that closely related species may display similar life-history traits because of shared ancestry (Felsenstein 1985). We therefore included phylogeny in the analysis using phylogenetic trees obtained from Jetz et al. (2012; <http://birdtree.org>) and the Hackett et al. (2008) backbone. A majority rules consensus tree was derived from a set of 1000 randomly-selected trees, which we then pruned to include only our 37 species of interest (Figure B.3). We used this consensus tree to specify values for the phylogenetic correlation matrix and then fit a general least squares model to the data to find the maximum likelihood value for Pagel's λ (Pagel 1999). Estimates of λ approach 0 if data are distributed independent of phylogeny and 1 when trait variation between species is proportional to their shared evolutionary history (Pagel 1999).

To account for both potential effects of phylogeny and indirect effects of mass on BMR and survival and elevation on BMR, we used a phylogenetic path analysis (PPA). PPA is an extension of multiple regression to assess direct and indirect paths among variables as well as the relative importance of various causal models while also incorporating the expected covariance due to shared ancestry (von, Hardenberg and Gonzalez-Voyer 2013). Model fit of PPA was evaluated using Fischer's C statistic to test whether the correlation structure observed in the data fits a set of minimal conditional independencies given by a causal model (Shipley 2000). A significant C statistic indicates that the model fit is poor (von, Hardenberg and Gonzalez-Voyer 2013). To facilitate comparisons between non-nested models, an analogous approach to model selection with QAIC_C can be employed based on the C statistic and is referred to as CIC_C (von, Hardenberg and Gonzalez-Voyer 2013). As with QAIC_C, models within 2 CIC_C are considered to be competitive with the top model if they had the same or fewer parameters with minimal change in the GOF estimate (Burnham and Anderson 2002, Arnold 2010).

We developed six models that explored different causal relationships among variables based on theoretical and empirical evidence. Specifically, we developed hypotheses testing scenarios in which BMR, elevation or both had a direct effect on apparent survival and whether an indirect effect of elevation on BMR improved model fit (Fig. 1). Well-established relationships between body mass and BMR (Londoño et al. 2015) and body mass and survival (Speakman 2005, McCarthy et al. 2008) were included in all tested models. By incorporating a causal link with mass, we accounted for allometric effects of body mass on both BMR and survival (von, Hardenberg and Gonzalez-Voyer 2013). We calculated the C statistic, CIC_C, and standardized path coefficients and associated 95% confidence intervals from each model using PGLS with an error structure following Pagel's λ (Pagel 1999). Compared to the best supported

model, which accounted for 56% of model weights, all competing models were >2 CIC_c larger or included additional noninformative parameters (Table 3.1). We therefore present results from only the top model H3 (Figure 3.2), although results of coefficients averaged over all models were qualitatively the same. All PPA were conducted with *R* using the `phylo_path` function in *phylopath* (van der Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013).

3.3 Results

3.3.1 Mark-recapture analysis

Mean annual survival probability for all species based on their top models was 0.50 with a standard error of 0.10. For families of birds represented by more than one species, survival probability was highest in Turdidae (mean $\phi = 0.56$, SE = 0.07), lowest for Troglodytidae ($\phi = 0.42$, SE = 0.03), and ranged most widely within the Thraupidae (range of $\phi = 0.35$ – 0.70 ; Figure 3.3, Table B.7). Not all families of birds were equally represented across the elevational gradient in our dataset, with some (e.g., Thraupidae, Parulidae) only occurring above 1000 m and others (e.g., Thamnophilidae) in lowland habitat. Of the 37 species, estimates of apparent annual survival were highest for *Pipra fasciicauda* ($\phi = 0.72$, SE = 0.13) and lowest ($\phi = 0.34$, SE = 0.13) for *Myiothlypis bivittata* (Figure 3.3, Table B.7).

3.3.2 Covariation in survival, basal metabolic rate, and elevation

Accounting for effects of phylogeny, body mass, and elevation, we found that BMR maintained a significant negative association with survival ($\beta = -0.76$, 95% CI = -1.23 to -0.05; Figures 3.4a and 3.4b). Similarly, when elevation was modeled as a direct effect, survival was higher for species living in lowland versus montane habitats ($\beta = -0.75$, 95% CI = -1.28 to -0.08; Figure

3.4c). Model structures that incorporated an indirect effect of elevation on survival via BMR, however, received little support relative to models that assumed independence between elevation and BMR (Table 3.1). Body mass also had a strong significant effect on BMR ($\beta = 0.90$, 95% CI = 0.74 to 1.01; Figure 3.4d), and a weaker, nonsignificant effect on survival ($\beta = 0.48$, 95% CI = -0.25 to 1.08; Figure 3.4e). Estimates of Pagel's λ were low (-0.11) indicating that there was little effect of phylogeny on survival.

3.4 Discussion

We found that for a phylogenetically diverse group of Passerine birds representing 10 avian families, apparent survival was negatively related with BMR and elevation (Figure 3.4a and 3.4c). This means birds with low BMR and living at low elevation showed the highest apparent annual survival, on average. Path models incorporating an indirect effect of elevation on apparent survival fitted the data poorly. Thus, although high elevation birds had similar BMRs to those at low elevation, we found no clear benefit of living at higher elevation in terms of apparent survival. As expected, we also found a positive, allometric relationship between body mass, BMR, and apparent annual survival. These results were unchanged when averaging effects over all path models, or when conducting path analyses ignoring phylogeny. Together, these observations suggest a functional link between BMR and survival in tropical birds, which exists independent of a species' elevational distribution, body mass, or phylogenetic history.

BMRs used here were a subset of estimates for 253 species of tropical birds, which showed no association between BMR and elevation (Londoño et al. 2015). In contrast, high-elevation bird populations in temperate regions exhibited higher BMRs than birds in lowland populations (McNab 2009). One reason BMR might vary with elevation is that thermoregulatory

costs are thought to increase at high elevation due to lower temperatures. For example, avian BMR increased 50% over a 20 °C decrease in temperature across latitudes (Jetz et al. 2008a). At our study area, daily mean temperature decreases by ~0.55 °C for every 100 m increase in elevation (Rapp and Silman 2012). Several reasons may account for the lack of relationship between elevation and BMR in the birds we studied. First, birds have adapted to cold climates largely independent of body mass via coordinated changes in BMR and thermal conductance (i.e., as the rate of heat gained from or lost to the environment; Fristoe et al., 2015). These physiological traits vary in a compensatory way; for example, although birds at Wayqecha (>2500 m) expressed similar BMRs to those at Pantiacolla (<550 m), the former had reduced thermal conductance (i.e., better insulation) and lower body temperatures (Londoño et al. 2017), suggesting higher resistance to heat loss. More generally, physiological adaptations to high elevations may not be obvious in standard field measurements of tropical birds such as BMR (Londoño et al. 2015) or thermal tolerances (Freeman 2015). Although BMR is the one of the most frequent and repeatable measures of energy expenditure, it accounts for only a portion of total energy used. Measures such as field metabolic rate (FMR) or thermogenic capacity may therefore better reflect energetic conditions experienced by birds daily (Daan et al. 1990). While BMR tends to covary positively with FMR (White and Seymour 2004) and exercise-induced metabolism (Wiersma et al. 2007a), it does so with high variability. Furthermore, measurements of FMR are particularly sparse for tropical birds (Anderson-Teixeira and Jetz 2005) with only a handful (<5) available for birds from humid montane forests such as those found at our study sites.

Although we detected no indirect effect of elevation via BMR, apparent survival was lower for highland birds. This was unexpected as many avian predators such as raptors (Thiollay

1996) and snakes (McCain 2010) decline with elevation. Predation rates are an important driver of both juvenile and adult survival (Martin 1995b) and are thought to be lower for birds living at higher elevations (Badyaev and Ghalambor 2001, Jankowski et al. 2013a). It is possible that low predation rates at high elevations are offset by higher adult mortality due to a harsher environment. For instance, male White-ruffed Manakins (*Corapipo altera*) at high elevations in Costa Rica exhibited greater physiological stress after major storms compared to lowland males (Boyle 2008). As far as we are aware, no studies examining demographic processes and other characteristics of the physical environment known to covary with elevation, such as temperature, partial pressure of oxygen, wind, and ultraviolet radiation, exist between high and low elevation populations of tropical birds. Some evidence of higher survival at high elevations is supported by case studies at north temperate latitudes (Badyaev 1997, Sandercock et al. 2005, Bears et al. 2009). However, in a review of intraspecific variation of life history traits, Boyle et al. (2016) found that studies reporting higher versus lower survival for high-elevation birds were nearly equally represented in the literature — 37% of comparisons showed a significant decrease in survival with elevation, whereas 42% showed increases. Overall, these contrasting results underline a species-specific variability of survival in response to environmental conditions that may differ depending on the geographic region and taxa considered.

For most tropical birds, survival estimates and other measures of life history traits from the field remain unknown; a fact that has limited our ability to address critical questions regarding the evolution and association of life history traits (but see Martin, 2015; Williams et al., 2010). Like other studies, our estimates of avian survival contain considerable uncertainty, but these survival probabilities remain the best estimates currently available for tropical birds (Williams et al. 2010). Studies reporting apparent annual survival for the same species of birds as

our analysis were similar, and most showed overlapping confidence intervals (Figure B.4) suggesting that our survival estimates are robust. Despite this, we found mean apparent survival of tropical birds was ~10% lower ($\phi = 0.50$, SE = 0.10) than values reported elsewhere from South America. Lower mean apparent survival may be explained by differences in survival rates between species captured above 1000 m (mean $\phi = 0.46$, SE = 0.08) versus those at lower elevations (mean $\phi = 0.55$, SE = 0.09). For example, apparent survival was higher for most lowland species, compared to their closely related congeners occurring at higher elevations (e.g., *Leptopogon amaurocephalus* versus *L. superciliaris*, *Mionectes oleagineus* versus *M. olivaceus*, *Lepidothrix coronata* versus *L. coeruleocapilla*; Figure 3.3, Table B.7), although this pattern did not always hold (e.g., *M. striaticollis*). When considering apparent survival of lowland birds alone, mean survival from this study is similar to those from Brazil (Wolfe et al. 2014), Cocha Cashu, Peru (Francis et al. 1999), Ecuador (Blake and Loiselle 2008), and French Guiana (Jullien and Clobert 2000). Methodological differences including the size of study plots, netting effort per plot, as well as geographic variation in survival could also have contributed to the differences we observed. Comparisons of survival of high-elevation species was not possible with these other Neotropical datasets, which were conducted over a limited elevational range in lowland tropical forest.

Several caveats merit additional consideration when interpreting the biological significance of our results. First, there is a growing appreciation for the intraspecific variation in BMR due to phenotypic flexibility (McKechnie 2008). Specifically, individuals may adjust BMR as a component of seasonal acclimatization, in response to breeding, or during migration (McKechnie 2008). While variation in BMR is expected to be low for species living in more thermally stable climates (Pollock et al. 2019), such as the tropics, metabolic measurements of

tropical birds from the rainy season are essentially unknown. In addition, significant geographic variation in BMR (Londoño et al. 2015) and survival (Wolfe et al. 2014) also exists, and could lead to mismatches in physiological and life history traits if drawn from populations experiencing different ecological conditions. While we were able to control for the latter of these possibilities, seasonal variation in BMR may have confounded our ability to detect its underlying relationship with survival. Second, variation in local movements of species with elevation could be an alternative explanation for the observed variation in apparent survival. Low estimates of apparent survival for some species may have resulted from low site fidelity, particularly for frugivorous birds that often make wide-ranging movements in search of food (Martin and Karr 1986), such as *Iridosornis jelskii* ($\phi = 0.40$, SE = 0.16), and *Euphonia xanthogaster* ($\phi = 0.37$, SE = 0.11). Another feature common to tropical birds that could lead to their permanent emigration is altitudinal migration. Although our understanding of the birds that undertake seasonal altitudinal movements is far from complete, >500 species of altitudinal migrants are currently described from the Neotropics, of which the majority are also frugivores (Merkord 2010, Barçante et al. 2017). For example, our estimate of apparent survival for *Chiroxiphia boliviana* ($\phi = 0.39$, SE = 0.16), a frugivorous altitudinal migrant (Villegas et al. 2016), was between 28–85% lower than other sympatric manakin species. Finally, we note that in our study area Londoño et al. (2015) showed that non-passerines had BMRs about 12 % lower than passerines, suggesting non-passerines should also express higher apparent survival than passerines on average. High apparent survival in the near-passerine *Galbula albirostris* (Piciformes) provides some support for this view (Wolfe et al. 2014), but additional empirical work will be needed to test whether negative relationships between BMR and apparent survival exist in avian species with dramatically different physiological and ecological life-history traits.

These caveats aside, our finding of a negative relationship between BMR and apparent annual survival in 37 species of tropical passerines provide evidence for the model of allocation trade-offs between slow-fast life histories. Our results support two main conclusions. First, BMR appears to be an intrinsic characteristic of the slow ‘pace-of-life’ of Neotropical birds and may not be as closely linked to temperature at low latitudes, as has been demonstrated along temperate elevational gradients. Second, variation in ‘pace-of-life’ in tropical montane species appears to be expressed as an elevational gradient in survival, but with BMR varying little between montane and lowland species. If true, this finding suggests that no suite of life-history traits is optimal for coping with the harsher abiotic factors found at high elevations of tropical mountains. One potential explanation for this pattern is that species inhabiting high elevations may be taxonomically younger than lowland species (Hawkins et al. 2012) and have not yet adapted physiologically to the local environment, or, alternatively, if higher extinction rates at high elevations preclude species from physiological adaptations. We emphasize a greater need for future studies measuring survival of tropical birds, especially those that provide information on high elevation and non-passerine species, to increase our ability to understand the fundamental question of why some species live long and others short lives.

Table 3.1 Results of the phylogenetic path analysis (PPA) where k is the number of linear models tested, q corresponds to the number of parameters estimated, and C is Fischer's C statistic. Hypothesized causal models are ranked according to a theoretical information criterion (CIC_C), ΔCIC_C is the difference in CIC_C values between models, and w_i is the model weight. Causal models are depicted in Figure 3.2.

Model	K	q	C	CIC_C	ΔCIC_C	w_i
H3	2	8	2.20	23.51	0.00	0.59
H6	1	9	0.75	25.42	2.07	0.21
H2	3	7	9.15	27.02	3.67	0.09
H1	3	7	10.51	28.37	5.03	0.05
H5	2	8	7.70	28.84	5.50	0.04
H4	2	8	9.06	30.20	6.85	0.02

Figure 3.1 Location of the three study sites adjacent to Manu National Park in southeastern Peru.

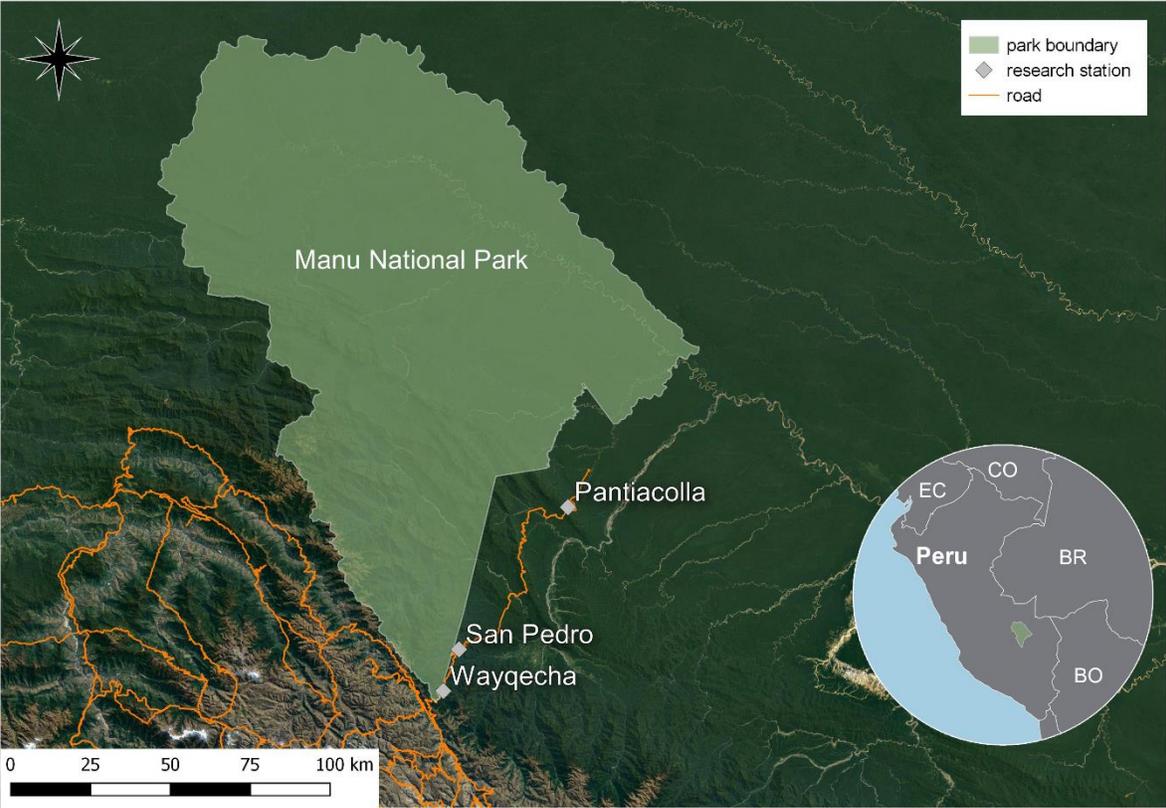


Figure 3.2 Conceptual framework used to test relationships among survival, physiology, and the environment (a), which suggests that a combination of metabolic costs and abiotic factors that vary between high and low elevations as well as allometric effects influence life history traits. For each alternative hypothesis (b), the predicted effect between variables is indicated as either positive (blue arrow), negative (red arrow), or a combination of both effects (blue and red arrow).

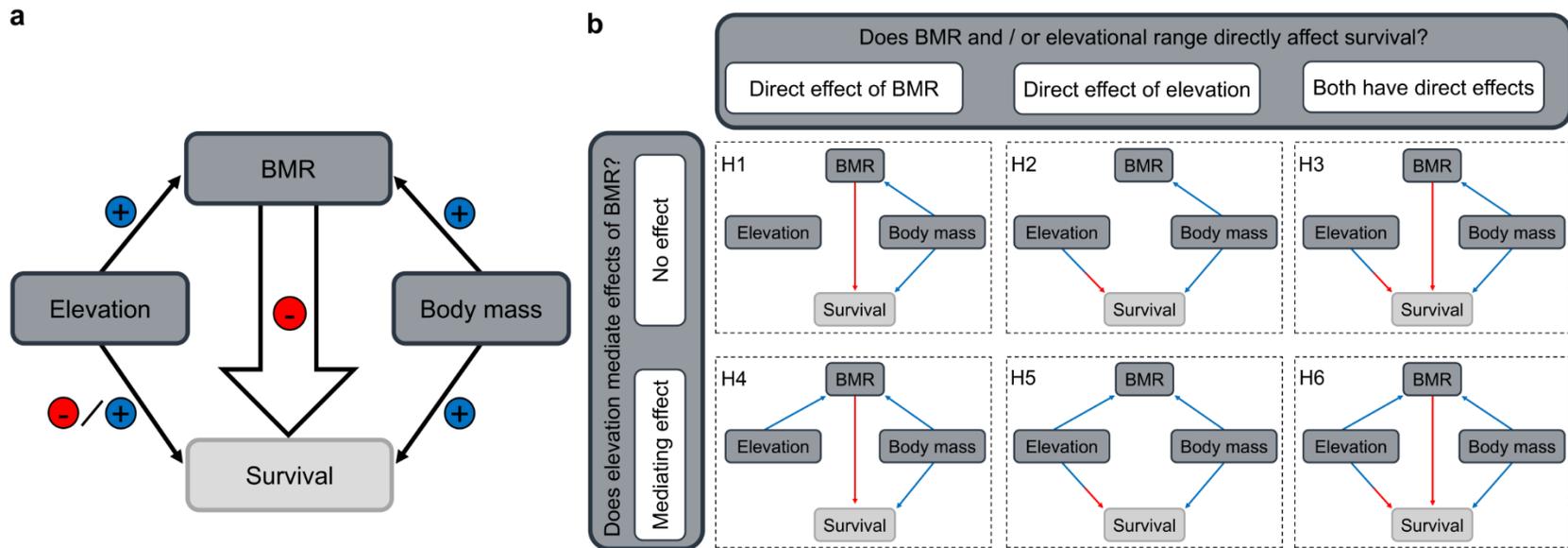


Figure 3.3 Apparent annual survival estimates and their associated standard errors for 37 species of tropical passerines from southeastern Peru.

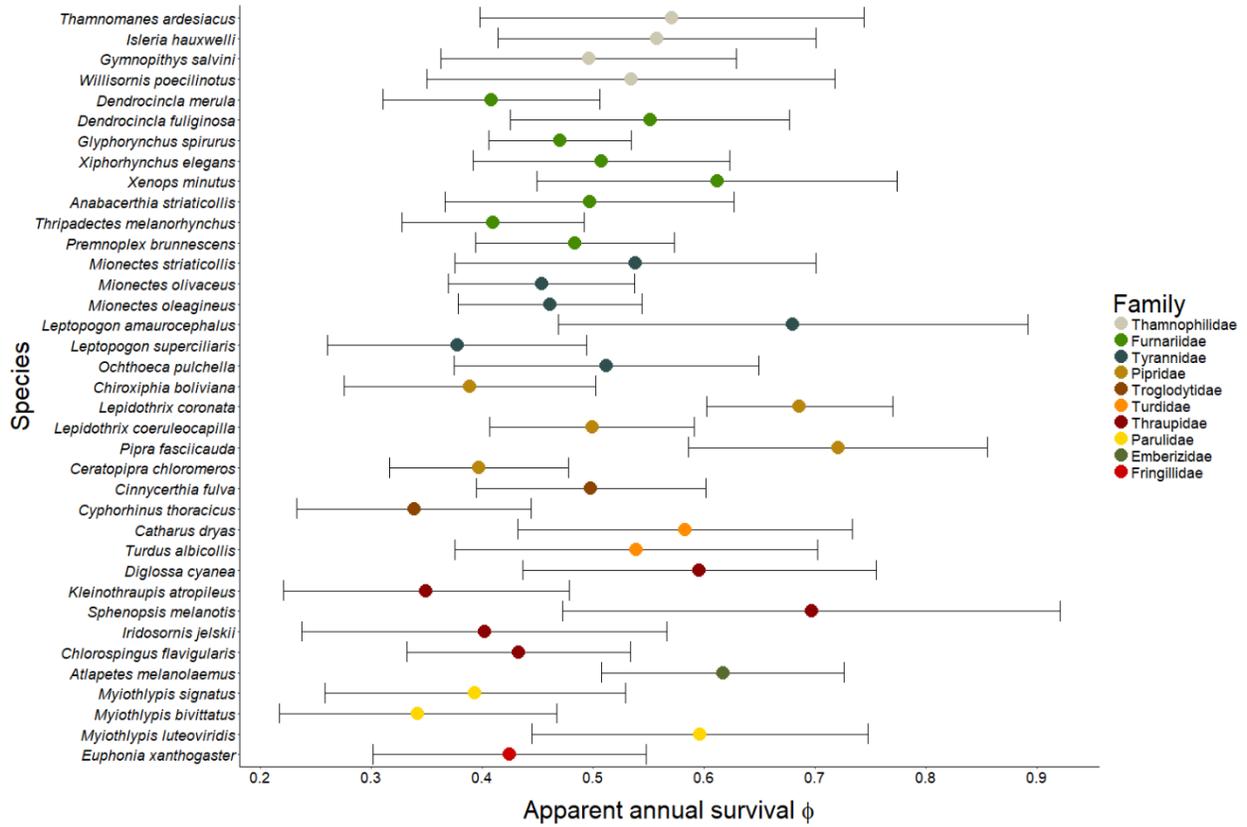
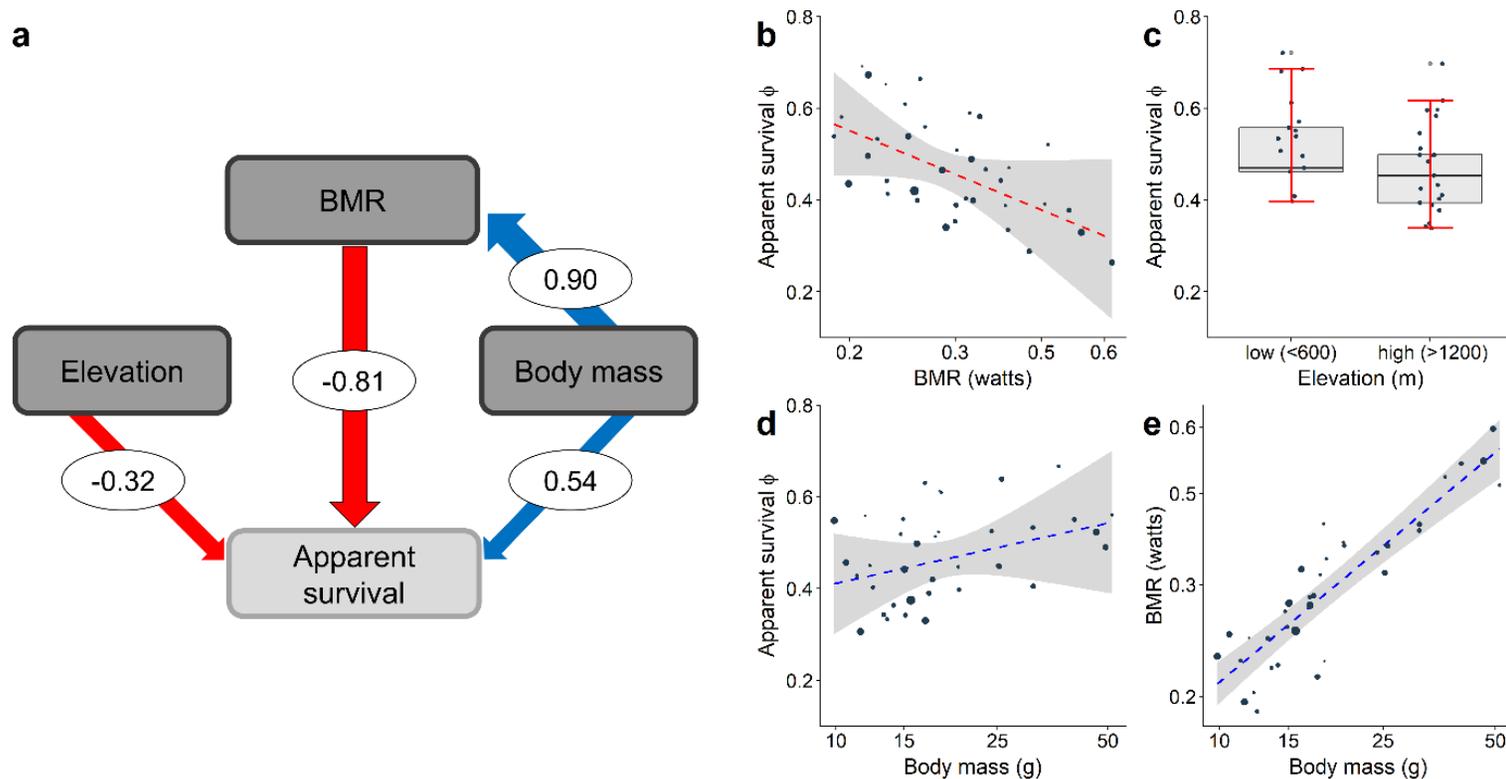


Figure 3.4 Best supported causal model from the phylogenetic path analysis (a). Arrows indicate the direction of the relationship between variables, arrow width indicates the strength of relationships, colors correspond to negative (red) or positive (blue) associations and values represent standardized regression coefficients. (b–e) Show the univariate linear relationships and associated 95% confidence intervals between survival and basal metabolic rate (BMR), the effect of elevation (coded as a binary variable) on survival, BMR and body mass and survival and body mass. Point sizes are drawn proportional to the inverse of their standard error.



Chapter 4: Molt limits as a tool for aging South American passerines

4.1 Introduction

The cyclical renewal of body and flight feathers is a life-history phenomenon shared by all birds. It is a costly process, both in terms of the energy required to produce feathers (Lindström et al. 1993, Guillemette et al. 2007, Bonier et al. 2007, 2018, Hoyer and Buttemer 2011) and the time needed for its completion (Hedenström 2006, Rohwer et al. 2009), but is necessary for the maintenance of plumage and its many functions (Newton 2009). Consequently, molt strategies have evolved to optimize the success of other energetically expensive activities within the annual calendar of birds, namely, breeding and migration. For example, most birds avoid overlap between molting and breeding because of decreased immune response during growth of new feathers (Moreno-Rueda 2010) and reduced flight performance (Swaddle and Witter 1997), which are presumed to interfere with reproductive success (Payne 1972). Similarly, the costs associated with feather growth are thought to preclude overlap between molt and migration, and different molt strategies have been shown to affect migratory timing of both New and Old World birds (Carlisle et al. 2005, Kiat and Izhaki 2016). Despite being a ubiquitous and critical stage in the avian life cycle, molt strategies and their resulting plumages have received disproportionately less attention than studies of breeding or migration (Newton 2009, Bridge 2011, Wolfe and Pyle 2012, Zuberogoitia et al. 2018).

In addition to providing insight into how birds balance the various costs of energetically demanding activities within their annual cycle, knowledge of molt is particularly valuable for monitoring wild populations. This is because molt cycles and their resulting plumages can be used to distinguish between individuals of varying age and sex classes, thereby providing a

useful conservation tool for understanding population structure (Skalski et al. 2005, Newton 2009). For instance, avian vital rates, such as survival and reproductive success, often covary with age (Stearns 1992), differ between males and females (Payevsky et al. 1997, Székely et al. 2014) and increase with advancing age for the vast majority of species (Martin 1995a). Ultimately, it is these age- and / or sex-dependent patterns in vital rates that drive the evolution of life histories and determine the population dynamics for a given species (McNamara and Houston 1996).

In passerines, all individuals molt at least part of their plumage during their first several months of life in what is referred to as the preformative molt (Wolfe et al. 2010). In many species, this includes replacement of most or all of the body feathers and a variable amount of wing and tail feathers (Jenni and Winkler 1994, Pyle 1997b, Newton 2009, Howell 2010). Whenever the extent of preformative molt is less than complete (i.e., when some of the juvenile feathers are not molted), aging birds can be accomplished by using boundaries between retained and replaced wing coverts, alulas, and flight feathers, known as ‘molt limits’ (Pyle 1997a). Although knowledge of molt is well developed in the northern hemisphere (Mulvihill 1993, Jenni and Winkler 1994, Pyle 1997b, 1998), far fewer data are available for how molt limits can be used for age classification in birds outside of Europe and North America.

Researchers have long known that plumage characteristics can be used to distinguish between cohorts of temperate birds (Stone 1896, Dwight 1900), but molt, plumage, and age-class differences in the tropics have been largely undescribed, even for widespread species (Rueda-Hernández et al. 2018). Much of our current understanding of tropical molt- and plumage-based age and sex criteria has been developed in the last 20 years (Rueda-Hernández et al. 2018), partly as a by-product of long-term bird banding and monitoring projects within the Neotropics (e.g.,

Lentino 2016; Johnson & Wolfe 2018; Kennedy *et al.* 2018). Museum specimens have also contributed a rich source information on tropical bird molt and have proved valuable in complimenting data collected in the field (Pyle *et al.* 2004, 2015, Wolfe *et al.* 2009, Guallar *et al.* 2018). Like many temperate species, tropical passerines often have an incomplete or partial preformative molt (Wolfe *et al.* 2010, Wolfe and Pyle 2012), making molt-based aging criteria possible through identification of molt limits. However, despite advances in our basic understanding of molt in the tropics, and the development of common protocols for its evaluation and measurement, collection of molt data has been slow to gain traction within the tropical ornithological community. One aim of this study, therefore, is to demonstrate the feasibility of collecting data on molt, as well as the necessity, given its importance for investigating population demography in poorly known tropical species.

Here, we conduct a literature review to assess the number of South American species with existing information on the preformative molt, with the goal of describing the frequency and occurrence of molt limits and their utility for age classification. As a case study, we demonstrate how knowledge of molt can be used to distinguish between juvenile and adult birds in seven species of manakins (family: Pipridae). Manakins provide an excellent example for species in which correctly assigning age classes is relevant because 1) young males are often indistinguishable from females of all ages by plumage alone (Ryder and Durães 2005), 2) males have extremely low reproductive success early in life (McDonald 1993a, 1993b), and 3) significant age-related variation in survival exists for both sexes (Pearce-Higgins *et al.* 2007, Ryder and Sillett 2016). We conclude by providing recommendations for how researchers can contribute to documenting molt in species of Neotropical birds for which this information is currently unknown.

4.2 Methods

4.2.1 Literature review

To gauge our collective understanding of South American bird molt, we gathered information on molt and plumage from the published literature, restricting our search to perching birds (order: Passeriformes) that breed in continental South America. Using the Web of Science Core Collections (<http://apps.webofknowledge.com/>) and Google Scholar (<https://scholar.google.com/>), we searched online using combinations of the following terms: ‘molt’ (OR ‘moult’), AND ‘bird’, AND ‘South America’ in English, Spanish, and Portuguese. We conducted an additional country-specific search using these same terms, but substituting names of each of the 12 South American nations as the location. For each relevant publication, we reviewed author references to search for other studies reporting data on the preformative molt for South American birds. We also included unpublished data on mist-net captures from three banding stations in southeastern Peru, collected 2013–2016 (Scholer and Jankowski unpub. data; see section 2.2.2 Field data). For each species in each study, we recorded data on 1) species name 2) extent of the preformative molt (i.e., the quantity of replaced feathers) in the wing and tail, 3) location of molt limits, and 4) the country or region where the study was carried out.

We used this database to summarize the proportion of birds that displayed either a partial, incomplete, or complete preformative molt (Figure 4.1) using terminology suggested by Humphrey & Parkes (1959) and revised by Howell *et al.* (2003). A ‘partial’ molt extent refers to replacement of some to all the body feathers, a variable number of secondary coverts, but no flight feathers. Partial molts can also include one to all three tertials and a pair of central rectrices. An ‘incomplete’ molt is when all or most of the body feathers and at least some flight feathers, excluding the tertials, or all rectrices are replaced. When all feathers are replaced molt

extent is said to be ‘complete’. A subset of studies provided more detailed descriptions of the variation in extent of preformative molt. In these cases, we extracted information on where molt limits occurred, and the range of feathers molted in specific feather tracts. Following Pyle (1997a), we defined flight feathers as including the rectrices (i.e., tail), remiges (i.e., primaries and secondaries), and primary coverts. The position of flight feathers, along with the secondary coverts, are referred to as inner and outer relative to the body of the bird rather than proximal and distal, respectively.

4.2.2 Field data

We collected data on molt and plumage from field observations at three research stations located in the Manu Biosphere Reserve, Peru (see Figure 2.1 in Chapter 2). The highest elevation site, Wayqecha Biological Station (13° 11' S, 71° 35' W, 2900 m a.s.l.), is situated at the upper extent of montane cloud forest, and transitions to puna grasslands above tree line (i.e., >3100 m a.s.l.). San Pedro (13° 3' S, 71° 33' W) includes lower montane and cloud forest with large stands of *Guadua* spp. bamboo up to 1300 m. Pantiacolla (12° 39' S, 71° 14' W) is located at the base of the Andean foothills and contains a mixture of primary floodplain, secondary lowland, *terra firme*, and riparian successional rainforest. We used observations collected between 2013–2016 to develop detailed aging and sexing criteria for seven manakin species and described general information on the molt strategies for an additional 58 species, which we used in the literature review. We augmented our description of preformative molt in manakins with data collected in 2018¹ from an undisturbed lowland rainforest site, Cocha Cashu (11° 54' S, 71° 22' W). In each of these study areas, a rainy season occurs from November through March with highest rainfall in January and February, while May through July form the dry season (Rapp and Silman 2012).

¹ Data contributed by Blaine Carnes.

Annual temperatures average highest at lowland sites (~25°C) and decrease by roughly 0.55°C for every 100 m increase in elevation (Rapp and Silman 2012).

All observations were made from birds captured using mist-nets (12 x 3 m, 36-mm mesh). At each field station, we sampled ten plots consisting of 10–20 nets set at ground level and spaced 5–50 m apart. Plots were sampled for 2–3 consecutive days from ~0600–1600 h and visited at least once each year. Most plots were located along trails and positioned adjacent to one another, spanning elevational ranges between 385–575 m at Pantiacolla, 1250–1720 m at San Pedro, and 2515–2985 m at Wayqecha and 350 m at Cocha Cashu. We timed data collection to overlap with the end of the dry season and the beginning of the rainy season (August–November), which is also the breeding period for most birds in the region (Londoño et al. 2015).

Captured birds were marked with a uniquely numbered aluminum leg band, measured, and released. Measurements included natural wing chord, tail length to the longest retriex, bill length from nares to tip, and culmen width taken from the anterior portion of the nares (all in mm), and body mass (in g). We determined sex and reproductive status by brood patch, cloacal protuberance, or dichromatic plumage and noted the presence and location of molt limits, degree of skull ossification, and coloration of the iris, bill, and legs.

4.2.3 Species accounts

We selected seven species of commonly occurring manakins from the Manu Biosphere Reserve for analysis. For each species, we recorded the extent of active and completed molt with the goal of describing the variation in replacement pattern in the wing-feather tracts during the preformative molt. We were able to confirm the presence of age-specific molt and plumage patterns by observing recaptured birds across multiple years, among, and within seasons.

Prealternate molts that result in the equivalent of a ‘breeding’ plumage (i.e., those found in some North American wood warblers and finches) have not been documented in Pipridae (Ryder and Wolfe 2009) and are therefore not considered here.

We aged birds using the methods developed by Wolfe, Ryder, and Pyle (i.e., the W-R-P system; Wolfe et al. 2010), which is based on two tiers of coding that first identify a bird’s molt cycle and then its plumage phase. For example, a juvenile in its first molt cycle (i.e., having grown its first set of pennaceous feathers) would be termed FCJ where ‘FC’ represents first-cycle and ‘J’ is juvenile plumage. If this same individual were molting into formative plumage, we would replace the ‘C’ with ‘P’ to indicate that it is undergoing the first ‘prebasic’ molt; termed FPJ (Johnson et al. 2011). In many passerines, the subsequent molt is a partial preformative molt resulting in formative plumage, and would thus be coded as FCF for ‘first-cycle formative’ plumage. Following this, molt cycles are typically complete (i.e., all flight feathers and coverts are replaced during a single cycle) and are referred to as ‘definitive-cycle basic’ plumage or DCB. An exception to this rule is when species have delayed plumage maturation, requiring one or more additional years to acquire the adult / definitive plumage aspect. In manakins, delayed plumage maturation is known to occur within males only of sexually dimorphic genera such as *Pipra* and *Chiroxiphia* (Ryder and Wolfe 2009). In these cases, male age classes can be further refined as ‘second-cycle basic’ (SCB) for individuals showing a mix of formative and adult like plumage and ‘after second-cycle basic’ SAB for those birds showing definitive plumage. Note that the code SAB is synonymous for DCB in birds that require more than two years to reach the definitive plumage. Table 4.1 provides a summary of the W-R-P coding for manakins considered in this study.

4.2.4 Age and sex specific measurements in manakins

We tested for the ability of morphological characteristics to distinguish between males and females and between FCF and DCB plumage birds using a multivariate analysis of variance (MANOVA) and Pillai's Trace statistic in R (v.3.5.3; R Core Team 2019). Specifically, we examined whether differences between wing chord, tail length, bill width, bill length, and body mass can be used to predict sex and age of individual manakins. Prior to analysis, we removed body mass measurements of gravid females (i.e., those noted to have an egg developing in the oviduct) and replaced them with the mean value for that species. We then examined all morphometric measurements for normality and homoscedasticity and found that they met the assumptions of a parametric test. Because not all manakins in formative plumage can be reliably sexed, we used only adult birds (i.e., birds in definitive plumage) for comparison of sex specific morphometric measurements. Similarly, we pooled sexes before examining difference in morphometrics between age classes. We used a sample of size of >15 individuals represented by each group (i.e., sex or age class) for inclusion in the analysis.

4.3 Results

4.3.1 Data available on molt and plumage for South American passerines

Of the 1,940 passerines listed for South America (Gill and Donsker 2019), we were able to locate information from 27 sources (Table C.1) on the extent of preformative molt for 287 species.

Multiple accounts were available for 41 species (n = 333 total species accounts) with as many as four studies reporting data for common species, such as *Volatinia jacarina* and *Zonotrichia capensis*. We found molt studies reported from 7 of the 13 South American nations (Table C.1). Descriptions of preformative molt were most commonly available from Brazil, Colombia, and

Peru, and no studies were found from Bolivia, French Guiana, Guyana, Paraguay, Suriname, or Uruguay.

The majority of passerines (64.8%) displayed a primarily partial preformative molt (n = 186), followed by complete (n = 76, 26.4%) and incomplete molt extents (n = 35, 12.2%). We found discrepancies in the molt extent reported for 3.5% of species (i.e., sources listed different patterns in the number and type of feathers replaced during the preformative molt; Appendix A.2), and 14.0% showed evidence of displaying more than one category of molt extent, most commonly a partial-incomplete replacement pattern. For 150 species with either partial or incomplete molts, we were able to locate more detailed information on where molt limits occurred. Of these, molt limits were most commonly noted within the greater coverts (79.2%) when preformative molt extent was partial and between the greater and primary coverts for species with an incomplete molt (63.2%). Molt limits within the primary and secondary flight feathers were also reported in 57.9% of species with an incomplete molt. Rectrices provided useful aging criteria for 41 of the 150 species (27.5%) with less than complete molts, but limits were only consistently present in 4 of these species. For a small number Tyrant Flycatchers (n = 7), molt limits were present between the median and greater coverts, and molt limits within the median coverts were found for most of the tropical Thrushes.

4.3.2 Molt sequences and morphometric differences by sex and age of manakins

All of the manakin species we studied exhibited a partial preformative and complete definitive molt cycle. Presence of molt limits within the greater coverts facilitated separation of formative- and definitive-plumage individuals for each species (Figure 4.2). At least two species, *Pipra fasciicauda* and *Chiroxiphia boliviana*, regularly showed evidence of delayed male plumage

maturation until after their third year of life. Sample sizes by age classes and morphological measurements for all species are summarized in Tables 4.2 and 4.3, respectively. We had sufficient data to test the utility of morphology in distinguishing between sex and age classes for four species. Mass was the most useful characteristic to separate males from females; females were always larger than males (Table 4.4). Bill length and width were also helpful in separating sexes, and were also always larger in females for 3 of the 4 species. In contrast, wing chord was longer in males. Differences in morphometrics between FCF and DCB birds were more idiosyncratic, but tail length appeared as a significant predictor for each species (Table 4.5).

4.3.3 Species accounts

4.3.3.1 Band-tailed Manakin (*Pipra fasciicauda*)

In our study areas, males show delayed plumage maturation through the third prebasic molt (Figure 4.3a–c), as suggested by (Robbins 1983) and similar to other members of the genus (i.e., *P. filicauda*, Ryder & Durães 2005; Ryder & Sillett 2016). The preformative molt is partial and includes all body feathers, lesser, and median coverts, between 3–10 greater coverts (median = 7), and occasionally the carpal and alula coverts, lesser and greater alulas, tertials, and up to three inner rectrices (Figure 4.2). The second and subsequent prebasic molts are complete. Females differ from males by having significantly greater mass as well as wider bills and shorter wings; although, these latter two characteristics show a high degree of overlap with males (Table 4.4). Juvenile plumage is dull green, with a yellowish wash on the throat, belly, and underwings. Iris color is gray-brown, the bill is dark with a pinkish base, and the skull is unossified.

The FCF plumage is olive green with distinct molt limits in the greater coverts (Figure 4.3a). Replaced greater coverts are brighter green contrasting with the dull green and yellow

washed juvenile feathers, have a higher density of barbules, and extend 2–3 mm beyond the retained juvenile greater coverts. Iris color ranges from pinkish to white and the upper mandible of the bill generally appears gray with a pale base while the lower mandible is mostly pale. The skull is ossified in most birds ($n = 7$) but may retain windows $<2\text{mm}$ through the FCF ($n = 1$). Males can often be identified by the presence of red feathers on the crown, nape, and around the eye as well as a white iris, although females can also have a whitish iris in FCF plumage. However, plumage maturation is highly variable in Pipridae (Ryder and Durães 2005) and FCF males may show female-like plumage aspect, lacking red feathers entirely. Birds having all green plumage should therefore be sexed as “unknown”, rather than female.

The SCB plumage of males appears intermediate between FCF and the definitive plumage (Figure 4.3b) and includes a reddish crown, nape and collar, yellow throat, breast and belly, and a variably shaded black back with a mixture of olive-green feathers. Coverts, flight feathers, and rectrices contain a mixture of olive green and definitive-like black feathers. Flight feathers of SCB males differ further from definitive plumage males by having less well developed white inner webbing and usually (always?) a block of replaced feathers that lack black coloration completely, resembling the formative plumage (Figure 4.3b). The third prebasic molt results in the definitive plumage (coded as SAB; see Table 4.1) and consists of a bright red crown, nape, and sides, and yellow forecrown, throat, breast, and belly that contrast sharply with jet-black back, coverts, and rectrices (Figure 4.3c). The flight feathers are black and have a distinct white patch on the inner webbing that forms a band across the entire wing. Bill color is dark gray fading to a lighter silver along the tomia and the iris is white.

As in other manakins, females attain DCB plumage following their second prebasic molt (Figure 4.3d–e). Replaced body feathers of the head, back and upperparts, as well as the coverts

and flight feathers are yellow-green and the throat, breast, and belly are yellow. Although adults of both sexes have a white iris, the iris of females often has a pinkish hue with a grayish ring around the periphery. Some DCB females acquire a few red feathers on the head and, in one case, several secondary flight feathers with white inner-webbing typical of DCB males (Figure 4.3e).

4.3.3.2 Round-tailed Manakin (*Ceratopira chloromeros*)

Molt patterns are similar to those described by Johnson & Wolfe (2018) for *C. erythrocephala*. The preformative molt is partial and includes all body feathers, lesser and median coverts, and between 2–10 greater coverts (median = 5; Figure 4.2). Occasionally, the carpal and alula coverts, lesser alula, and one to two tertials are replaced, but rectrices appear to be retained. Definitive prebasic molts are complete. Females measure significantly larger for all the morphometrics we considered except wing chord (Table 4.4). Juvenile plumage is dull green with a dusky wash to the coverts, flight feathers, and rectrices. Iris color is gray, the bill is dark with a pale flesh-colored base, and the skull is unossified.

Birds in formative plumage are olive green overall and have molt limits among the greater coverts (Figure 4.4), which are brighter colored, longer, and more densely textured than retained juvenile greater coverts. Iris color begins to lighten in both sexes and ranges from gray to white. The bill is flesh-colored with a variably dark tip to the upper and lower mandibles, which helps with separation from FCF *P. fasciicauda*. The skull remains unossified until sometime shortly after the preformative molt (FPF / FCF skull = 4, n = 2), but is complete in most birds (FCF skull = 6, n = 10). Some FCF males (n = 12) develop traces of red feathers on the head and/or black body plumage, as well as white flecking on the pale-gray iris or a

completely white iris. Individuals with all green plumage and lacking male characteristics should be sexed as unknown.

Males in DCB plumage replace olive-green feathers with bright red head feathers, black body and flight feathers, and yellow leggings, and have a white iris and a mostly pale bill (Figure 4.4c–d). Occasionally, some males ($n = 2$) may be aged as SCB based on presence of a few retained green juvenile feathers on the flanks and axillaries. Females replace relatively dull and dusky-washed primary coverts and flight feathers with olive-green feathers and DCB plumage is distinguished from FCF by the uniform, broad, and relatively fresh greater and primary coverts, and lack of molt limits (Figure 4.4e–f). As in FCF males, 14% of the DCB females we captured had white flecking to the iris and small amounts of red feathers around the orbital, chin, crown, and nape (Figure 4.4e).

4.3.3.3 Blue-crowned Manakin (*Lepidothrix coronata caelestipileata*)

Molt and plumage sequences in *L. c. coronata* are described for black-bodied populations in Ecuador (Ryder and Durães 2005). Adult males in populations inhabiting Madre de Dios are green-bodied with blackish faces. Irrespective of taxonomic affinity, *L. c. caelestipileata* appear to follow a similar pattern of plumage development as individuals of *L. c. coronata*. The preformative molt is partial and includes all body feathers, lesser and median coverts, and between 3–8 (median = 4) greater coverts. Occasionally FCF individuals replace the carpal covert and, rarely, the alula covert and lesser alula (Figure 4.2), but tertials and rectrices appear to be retained. Definitive prebasic molts are complete. Females have significantly greater mass and bills (both width and length) while males average longer wings (Table 4.4). Juvenile

plumage individuals have dull green upperparts and wings with a pale-yellow breast and belly. The iris is dark brown. The bill is black with a fleshy gape, and the skull is unossified.

Birds in FCF plumage have green upperparts and breast, a pale-yellow throat and belly, and molt limits in the greater coverts (Figure 4.5a–b). Replaced greater coverts are brighter green, longer, and more densely textured than retain juvenile greater coverts, and formative remiges have comparatively narrower and duller green edging than replaced basic feathers. The iris is brown to reddish brown and the bill is dark with a pale gray base that often extends onto the lower mandible. The skull retains windows <2 mm in some FCF birds (skull = 4–5, n = 7), but is often ossified (n = 14). Many males develop small amounts of electric blue feathers on the crown or around the eye (n = 6) and, in two cases, blue-green edging on replaced greater coverts and flight feathers. All green birds with molt limits should be sexed as unknown, rather than female, as some FCF males never develop these characteristics.

DCB Males replace green feathers of the head with an electric-blue crown and a sooty-black face (Figure 4.5c). Replaced body feathers are brighter green and flight feathers are blackish with bright green edging (Figure 4.5d). DCB females have FCF-like body plumage, but lack molt limits in the greater coverts and are brighter green overall (Figure 4.5e–f). As in FCF males, some (n = 9) DCB females have small amounts of blue feathers on the crown and may even develop a blueish hue to the inner greater coverts (n = 1). Differences in iris color are subtle between formative and definitive plumage individuals, but are generally a deeper reddish-brown in DCB individuals, especially in males.

4.3.3.4 Cerulean-capped Manakin (*Lepidothrix coeruleocapilla*)

Molt patterns of *L. coeruleocapilla* are like those of *L. coronata* and other *Lepidothrix* manakins throughout Amazonia (e.g., *L. serena*; Johnson & Wolfe 2018). The preformative molt is partial and includes all body feathers, lesser and median coverts, between 2–7 (median = 4) greater coverts and occasionally the carpal covert (Figure 4.2). Tertiaries and rectrices appear to be retained. Definitive prebasic molts are complete. Juvenile plumage is dull green with a pale-yellow belly, iris and bill are colored dark, and the skull is unossified.

Individuals with FCF plumage have green upperparts, yellow underparts, and molt limits among the greater coverts (Figure 4.6a–b). Like *L. coronata*, replaced greater coverts are brighter green, longer, and more densely textured than retained juvenile greater coverts. The iris is brown to reddish brown and the bill is dark with a pale gray base. Skull ossification likely completes sometime shortly after the preformative molt (FPF skull = 3, n = 1), with some FCF birds retaining windows <2 mm (skull = 4, n = 3). Males may develop small amounts of electric blue feathers on the head and rump. As in the other manakin species discussed, all green birds with molt limits cannot be reliably sexed because not all FCF males develop these characteristics.

Males replace green feathers with an electric blue crown and rump patch, and black body and flight feathers (Figure 4.6b–d). Delayed plumage maturation permits some males (n = 3) to be aged as SCB based on greenish edging retained on otherwise black covert and/or secondary flight feathers (Figure 4.6e). DCB females resemble FCF plumage, but lack molt limits in the greater coverts and are brighter green overall (Figure 4.6f–g). As in FCF males, some (n = 3) DCB females develop small amounts of blue feathers on the crown, nape, or rump (Figure 4.6g).

Differences in iris coloration are subtle with DCB individuals attaining a richer reddish-brown compared to FCF individuals.

4.3.3.5 Yungas Manakin (*Chiroxiphia boliviana*)

Like other members of the genus *Chiroxiphia*, male *C. boliviana* pass through a series of progressively more mature plumage changes, reaching definitive plumage after the third prebasic molt. The preformative molt is partial and includes all body feathers, lesser and median coverts, between 1–8 greater coverts (median = 4), and occasionally the carpal covert, alula covert, and lesser alula. Tertiaries and rectrices appear to be retained. Subsequent prebasic molts are complete. Although there was considerable overlap in the ranges for all measurements, females were significantly heavier and had longer bills, but males had longer wings (Table 4.4). Juvenile plumage is olive green with dusky green rectrices, coverts, and flight feathers, the iris is dark brown, the bill black, and the skull is unossified.

Birds in FCF plumage are brighter green overall compared to juvenile plumage and have molt limits in the greater coverts. Replaced all-green coverts contrast with retained and worn olive-green coverts (Figure 4.7a), which are sometimes tipped buff, perhaps only in young males? Iris color is dark to chestnut brown and the bill color remains black throughout successive molts. The skull appears to remain unossified (skull = 5, n = 13) for most FCF birds (76% of birds examined). FCF males can be identified by patches of blue-green edging on relatively worn retained flight feathers and the presence of red feathers on the crown, blue feathers on the back, and a variably developed black mask. Unlike other manakin species we studied, young males always appear to develop some degree of male-like plumage following the

preformative molt, which may allow observers to distinguish between sexes for most FCF plumage birds.

Like *P. fasciicauda*, SCB males appear intermediate in plumage to FCF and SAB individuals, and include a reddish crown, a variably shaded black body with a mixture of blue, green, or blue and green feathers on the shoulders, and a greenish wash to replaced coverts, rectrices, and flight feathers (Figure 4.7b). The third prebasic molt results in definitive (SAB) plumage for males and consists of a red crown, blue shoulders and scapulars, and all-black body, covert, rectrices, and flight feathers (Figure 4.7c). Females attain an olive-green definitive basic plumage following their second prebasic molt, which appears similar overall to formative plumage birds (Figure 4.7d–e). Some DCB females acquire blue-green edging to the coverts and flight feathers (Figure 4.7e), probably only in older birds.

4.3.3.6 Fiery-capped Manakin (*Machaeropterus pyrocephalus*)

Molt and plumage in the genus *Machaeropterus* is largely undescribed. Like other manakins, the preformative molt is partial and includes all body feathers, lesser and median coverts, between 2–8 greater coverts (median = 3), occasionally the carpal and alula coverts, but no tertials or rectrices (Figure 2.1). Definitive prebasic molts are complete. The Juvenile plumage remains undescribed.

Birds in FCF plumage have olive-green upperparts, pale gray, green or whitish underparts, and molt limits in the greater coverts (Figure 4.8a–b). Replaced coverts are brighter green and more densely textured, and in the case of inner greater coverts, may have grayish shading on the inner webbing. In males, the greater coverts are graduated in size and increase distally. Thus, unlike most other species with a partial preformative molt, retained outer greater

coverts of FCF birds can extend beyond replaced inner feathers and should not be confused with molt limits. Iris color ranges from reddish orange to red in what are likely males, to gray in what are probably females. The bill is black with a pale base. Skull ossification likely completes sometime shortly after the preformative molt (skull = 6, n = 4; skull = <6, n = 2). Some FCF males (n = 12) have trace amounts of yellow and red feathers on the head and brown smudging on yellowish underpart (Figure 4.8a). Individuals lacking male characteristics should be sexed as unknown.

Males in DCB plumage have a golden cap with a central red stripe, a reddish-brown back, white underparts streaked rosy-brown, and an olive tail and wings with a silvery-white patch across the secondaries (Figure 4.8c–d). The eye is bright red and the bill is black with a dark-gray base. Females resemble FCF individuals, but lack molt limits (Figure 4.8e–f). Replaced coverts and remiges are brighter green and have more luster than the relatively dull and dusky-washed wing feathers of FCF birds. Some DCB females developed small patches of reddish-brown feathers on the rump (Figure 4.8f–g) and gray webbing on along the rachis of the inner secondaries.

4.3.3.7 Green Manakin (*Cryptopipo holochlora*)

Cryptopipo holochlora are sexually monochromatic and have reduced size dimorphism compared to other manakins (Ribeiro et al. 2015). The preformative molt is partial and includes all body feathers, lesser and median coverts, some inner greater coverts, and occasionally the carpal covert (Figure 4.2). Subsequent prebasic molts are complete. Juvenile plumage is undescribed.

Birds in FCF plumage have green upperparts and yellow-green underparts, with molt limits in the inner greater coverts (Figure 4.9a–b). Replaced greater coverts differ subtly from retained outer juvenile coverts, which are shorter, more loosely textured, and tinged yellow. The bill is black, and the iris color is dusky. One FCF individual had an ossified skull. In contrast to other manakin species, DCB individuals are similar in all aspects to FCF plumage, but appear slightly brighter green and have primary coverts and flight feathers that appear relatively fresh (Figure 4.9c–d). Because coloration is very similar between age classes of *C. holochlora*, tail shape is particularly useful for this species in distinguishing between FCF and DCB individuals, the former of which tend to more tapered, worn, and poorer quality in general.

4.4 Discussion

In this study, we showed that the majority of tropical species can be aged using molt limits by Our review of the literature summarizes information on the extent of preformative molt and variability of feather replacement for nearly 300 South American passerines. The majority of species in our literature review had less than complete molts, helping facilitate their age categorization through identification of molt limits. In particular, molt limits within the greater coverts or between greater and primary coverts were common. More than 90% of species that displayed either a partial or incomplete preformative molt could be separated by age class based on retention of juvenile plumage in one of these two feather tracts. In our case study examining the molt strategies in the family Pipridae supported the general patterns apparent in our literature review — namely, that molt limits involving the greater coverts were the most useful criteria for separating formative plumage from older age classes. Granted, species with cryptic molt patterns, such as some tyrant flycatchers (e.g., *Corythopis torquatus*, *Mionectes* spp.) and wrens

(e.g., *Troglodytes* spp.), will always present difficulties, our overall results suggest that most Neotropical passerines can be reliably separated into age classes using molt limits.

4.4.1 The current state of knowledge of molt in South American passerines

Accumulation of species-specific descriptions of molt and plumage in tropical birds has lagged behind progress made in North America and Europe (Ryder and Wolfe 2009, Rueda-Hernández et al. 2018), and our literature review indicates that basic molt data are still lacking for >85% of passerines that breed in South America. Our understanding of molt in tropical birds from Central America and the Caribbean, for which 34% of species had some information associated with the extent and / or timing of molt (Wolfe and Pyle 2012), fares somewhat better. Much of the information contributing to this higher percentage comes from long-term bird monitoring programs run in collaboration with the US federal government (e.g., US Fish and Wildlife) and NGOs (e.g., Kalamath Bird Observatory, Institute for Bird Populations), highlighting the importance of these international bird-banding partnerships (Rueda-Hernández et al. 2018). In contrast, far fewer long-term bird banding stations have been operated in South America (but see Johnson & Wolfe 2018), perhaps because of the reduced number of North American migrants and, hence, reduced interest from North American organizations in supporting such ventures. A number of Neotropical species covered in the review by Wolfe & Pyle (2012) have distributions that include both Central and South America (e.g., *Dysithamnus mentalis*, *Catharus fuscator*, *Turdus obsoletus*, *Euphonia anneae*), but were not included in our analysis because the study occurred outside of South America. Nevertheless, excluding those species with molt strategies described by Wolfe & Pyle (2012), we lack information on nearly 1500 species, or 75% of South American passerines.

4.4.2 The utility of molt limits in aging tropical birds

Using molt limits in the wing provides a practical and accurate method for age classification of tropical birds (Pyle et al. 2004, Ryder and Durães 2005, Johnson and Wolfe 2018). When considering those South American passerine species with information on the variability of feather replacement in the wings, our review suggests that a large portion (55%) with partial or incomplete molts almost always show molt limits in the greater coverts (i.e., most commonly molt between 5 to 6 greater coverts). Another 18% of species molt this entire feather tract, resulting in contrasts between retained primary and replaced greater coverts. Identification of molt limits within a single feather tract, such as the greater coverts, is often best for age discrimination because it provides a direct means of comparison between two generations of feathers, rather than between two sets of feather tracts, which may differ naturally in their shape, size, and color (i.e., between greater and primary coverts or secondary and primary flight feathers). Molt limits between or within the carpal covert and alula tract (i.e., the alula covert, lesser alula, and greater alula) also appear to be relatively common and are easily recognizable in tropical species (Johnson and Wolfe 2018, Kennedy et al. 2018), just as they are in some North American passerines (Rowe and Wolfe 2010). For instance, in our *Manu* dataset, we documented molt limits in the carpal covert for 17 species belonging to five families: Pipridae, Turdidae, Thraupidae, Emberizidae, and Parulidae. Molt limits within the median coverts, lesser coverts, and rectrices also provided a means of aging some birds, but were typically accompanied by more reliable indicators, such as contrast within the greater coverts.

In addition to molt criteria, we also found mention of other methods for assessing a bird's age, including degree of skull ossification, the color and texture of the bill, gape, mouth lining, eye, and tarsus, and the shape, size, wear, and color of feathers. In particular, skull ossification

can be useful for aging individuals as FCF when the extent of the preformative molt is complete, but skull ossification is incomplete (e.g., many Furnariids; Johnson & Wolfe 2018). However, the technique is often more difficult for inexperienced practitioners to apply than molt limits, and has the drawback of many tropical species retaining small (<2mm) unossified ‘windows’ in the skull throughout their lives (Johnson and Wolfe 2018). In addition, the presence of molt limits in tropical species may persist for longer than the skull remains unossified, as in some temperate species (Pyle 1997a). Overall, the most powerful tool available for aging tropical birds is the use of molt limits in concert with other criteria such as skull ossification, the color and texture of soft parts, and general plumage characteristics.

4.4.3 Age and sex criteria for manakins

We provide heretofore undescribed aging and sexing criteria for six species and one subspecies of manakin, bringing our collective knowledge of molt in Pipridae to nearly half of currently recognized taxa. Molt and plumage sequences in manakins have previously been documented for a number of species (Table C.2). Our findings generally conform to those of other researchers, and indicate that the preformative molt is partial and that males take between 1–2 years to attain definitive plumage. We were therefore able to differentiate individuals in formative plumage from older age classes by the presence of multiple generations of feathers in the wing, specifically within the greater coverts. These findings are yet another example of how tropical birds can be aged easily using techniques commonly applied in temperate regions.

We found delayed plumage maturation in two genera that have previously been described (i.e., *Pipra* and *Chiroxiphia*) and provide evidence that this condition may also exist within the *Ceratopipra* and *Lepidothrix* manakins. These data support the suggestion of Ryder & Durães

(2005) that acquisition of definitive plumage in males after three, rather than two, years may be relatively common. For instance, some accounts of plumage maturation in *P. fasciicauda* assumed males attain definitive plumage at the beginning of their second year (Pearce-Higgins et al. 2007). However, we show that individuals often resemble a mixture of FCF and DCB plumage following their second prebasic molt, as suggested by (Robbins 1983) and found in *P. fasciicauda*'s sister species, *P. filicauda* (Ryder and Durães 2005, Ryder and Sillett 2016).

Chiroxiphia manakins are well known for attaining definitive plumage later than other Piprids (Foster 1987, DuVal 2005, Doucet et al. 2007, Mallet-Rodrigues and Dutra 2012), typically between their third and fourth year, and our results for *C. boliviana* support this trend. Within the *Lepidothrix* manakins, Johnson & Wolfe (2018) speculated that some males of *L. serena* attain definitive plumage after the third prebasic molt. Our data suggest that this pattern may not be an anomaly — we found 20% of known males showed signs of a greenish wash on the body and wings after the second prebasic molt. Finally, we report the first case of delayed plumage maturation in *Ceratopipra*. Given that *C. chloromeros* was our most commonly captured species, we might expect to have detected this condition with a higher frequency than what we observed (i.e., only 2 males showed signs of delayed plumage maturation). Because predefinitive plumages are thought to function as age-specific status symbols (McDonald 1993a), species that irregularly delay plumage maturation, such as *C. chloromeros*, may simply reflect the occasional male that foregoes entering the breeding queue. By adopting this strategy, individuals that lack the energetic resources required to produce definitive plumage could still be identified as males and as subordinates, thereby allowing them to preform courtship displays while reducing risk of aggression from older males (Morales-Betancourt and Castaño-Villa 2018).

Although morphology was useful in separating males from females and FCF from DCB individuals, there was a high degree of overlap for nearly all the measurements we considered. Previous studies of manakins have found morphology is predictive of both age and sex (Ryder and Durães 2005). However, unlike Ryder & Durães (2005), who used molecular techniques to sex individual birds, we based our analysis of age on FCF and DCB birds of unknown sex. Thus, mean differences in the average wing chord, tail length, and mass found to be predictive between FCF and DCB individuals were likely confounded by an unknown mixture of male and female measurements. Furthermore, in each of the species considered in our analysis, a portion of females displayed male-like plumage. Male-like plumage in females has previously been reported for a number of manakin species (Graves 1981) complicating sex / age classification. This is because birds without molt limits and signs of male like plumage could either be young males or older females. For example, in some cases, males may not acquire any signs of definitive plumage until after third prebasic molt (Ryder and Durães 2005). Thus, our analysis of morphology should be interpreted with caution, as misclassification of sexes likely resulted in a source of error. Differences in manakin morphometrics do exist between males and females, and in juveniles versus adults (Payne 1984, Ryder and Durães 2005), and our analysis does not discount the utility of such measurements in classification. Rather, our findings suggest that morphology should be used to aid researchers in combination with information on molt limits and plumage characteristics to distinguish between sex and age classes.

4.4.4 Moving forward with molt in the tropics

Our current understanding of tropical molt indicates that the extent of preformative molt is relatively similar across latitudes (Wolfe and Pyle 2012), and that tropical passerines can be aged

in a manner similar to temperate species (Pyle et al. 2004, Ryder and Wolfe 2009, Wolfe et al. 2010). Armed with this knowledge, ornithologists must begin in earnest to develop quantitative descriptions of molt that remain undescribed for most tropical birds. While a species-by-species approach is ideal, a more practical goal might be to collect information on molt from representatives of each avian order and family. For example, while we have data for some 15% of South American passerines, almost nothing is known about molt in non-passerines, partly because these species occur at lower population densities and behave in ways that make them less likely to be captured by passive mist netting (i.e., occupying a higher strata within the canopy, nocturnally active, aerial insectivores). A broadscale approach to understanding molt in South America would not only enhance our ability to age birds for conservation-based monitoring (DeSante et al. 2015), but would help us to begin generalizing molt strategies for all tropical birds, and to answer ecological and evolutionary questions aimed at describing their origin and maintenance (Bridge 2011, Wolfe and Pyle 2012, Guallar et al. 2016).

Capacity building and international partnerships are another crucial ingredient moving forward with molt studies. For instance, the Institute for Bird Populations' (IBP) *Monitoreo de Sobrevivencia Invernal (MoSI)* has been successful at bringing together nearly 60 partners, representing academic researchers, government agencies, and non-profits, to monitor Neotropical migrant and resident birds across 14 Latin American countries (Saracco et al. 2009). The large geographic scale of these data has been invaluable not only for identifying conservation targets and priorities, but has contributed much to our understanding of tropical molt (Wolfe and Pyle 2012). Another example of successful international partnerships involves The North American Banding Council (NABC) and the Centro de Ornitología y Biodiversidad (CORBIDI), which began annual training workshops that teach Peruvian bird banders how to safely operate mist-

nets, mark captured birds, and collect information on their morphology, age, and sex (Díaz et al. 2019). These training opportunities are relatively new for countries such as Peru, despite these regions supporting some of the most diverse avian assemblages in the world (Jenkins et al. 2013). One way to increase the effectiveness of these partnerships is by making data on molt more accessible. In the last two decades, more than half of published molt studies were from North American authors, and nearly three-quarters of all studies were published in English (Rueda-Hernández et al. 2018). Clearly, we need to be doing a better job of making information on molt available to researchers fluent in languages other than English. For instance, a collection of recently published photographic guides on tropical molt strategies (e.g., Pyle et al. 2015, Johnson and Wolfe 2018) are opening the field of molt to a new generation of ornithologists, and translations of these into Portuguese and Spanish would be beneficial. Partnerships that promote a combination of accessible data and training workshops would help sustainably build expertise in the skills required to effectively and ethically work with captured birds, and, ultimately, further our collective knowledge of tropical molt.

Finally, we encourage those ornithologists whose projects may not directly relate to the study of molt to help collect data. There are many reasons why researchers may require the capture and examination of wild birds in the hand, and each of these represents an opportunity to add to our collective knowledge of molt in the tropics. Measurements such as wing chord, tail length, and mass are standard to record, and perhaps molt should be as well. Molt is relatively easy to collect, and standardized photos of the wing and tail can assist in confirming molt patterns at a later date. At a minimum, if researchers could place birds into categories of molting flight feathers or not molting, we could begin to understand the timing and duration of molt, providing that the population is sampled throughout the appropriate molting period. Many

researchers may already collect this information, and, in these cases, we encourage them to publish their findings. For instance, bird monitoring programs exist throughout the tropics of Africa and Australia, but information on molt from these regions do not. We hope that by describing the effectiveness of molt limits and plumage characteristics as age and sex classification tools, we can raise awareness of the importance of molt in contributing to conservation-based research and understanding the avian life cycle.

Table 4.1 A list of W-R-P molt-based aging codes used in this study. The equivalent codes for the calendar-based aging system commonly used in North America are shown for comparison. Note that for males, the code SCB will be replaced by DCB for species that acquire definitive plumage after the second prebasic molt. For species with delayed plumage maturation (i.e., *Pipra fasciicauda* and *Chiroxiphia boliviana*) ages of males can be further refined as TPB and SAB and only females are coded with DCB. A complete list of codes available for use with the W-R-P system can be found in (Wolfe et al. 2012).

W-R-P Code	Expanded W-R-P code	Calendar-based age	Applicable sex
FPJ	Prejuvenile molt	Hatch year	♂ ♀
FCJ	First-cycle juvenile	Hatch year	♂ ♀
FPF	Preformative molt	Hatch year	♂ ♀
FCF	First-cycle formative	Hatch / second year	♂ ♀
SPB	Second prebasic Molt	Second year	♂ ♀
SCB	Second-cycle basic	Second / third year	♂
DPB	Definitive prebasic molt	Third / fourth year	♂ ♀
DCB	Definitive-cycle basic	After second / third year	♀ / ♂ ♀
TPB	Third prebasic molt	Third year	♂
SAB	After second-cycle basic	After third year	♂

Table 4.2 Number of individuals captured in each age class for the seven species of manakins included in this study.

Species name	W-R-P age code										Total
	FPJ	FCJ	FPF	FCF	SPB	SCB	DPB	DCB	TPB	SAB	
<i>Pipra fasciicauda</i>			1	47	1	7	1	80		25	162
<i>Ceratopipra chloromeros</i>			1	41		2	4	136			184
<i>Lepidothrix coronata</i>	1	1	2	45			5	100			154
<i>Lepidothrix coeruleocapilla</i>			2	14		3		26			45
<i>Chiroxiphia boliviana</i>			1	26	3	5	4	22	1	27	89
<i>Machaeropterus pyrocephalus</i>				9			1	25			35
<i>Cryptopipo holochlora</i>				3			1	6			10

Table 4.3 Morphological measurements (mean \pm standard error) for seven species of Manakin (Pipridae) sampled from humid montane and tropical lowland forest in southeastern Peru. Length measurements are in millimeters; body mass is in grams. Note that some sample sizes differ from those reported for species accounts since not all measurements were collected from each captured bird.

Species name	Wing chord	Tail length	Bill width	Bill length	Mass	Sample size
<i>Pipra fasciicauda</i>	63.5 \pm 0.17	30.5 \pm 0.25	4.2 \pm 0.04	7.3 \pm 0.05	16.8 \pm 0.09	122
<i>Ceratopipra chloromeros</i>	61.3 \pm 0.14	27.0 \pm 0.16	4.3 \pm 0.04	6.9 \pm 0.05	16.8 \pm 0.09	165
<i>Lepidothrix coronata</i>	57.1 \pm 0.18	28.3 \pm 0.13	3.7 \pm 0.03	6.1 \pm 0.05	9.6 \pm 0.08	144
<i>Lepidothrix coeruleocephala</i>	53.8 \pm 0.31	25.7 \pm 0.31	3.4 \pm 0.06	5.4 \pm 0.07	10.4 \pm 0.13	42
<i>Chiroxiphia boliviana</i>	66.6 \pm 0.23	43.6 \pm 0.23	3.9 \pm 0.04	5.7 \pm 0.04	17.3 \pm 0.11	81
<i>Machaeropterus pyrocephalus</i>	52.9 \pm 0.45	22.7 \pm 0.22	3.6 \pm 0.08	5.5 \pm 0.09	9.9 \pm 0.10	33
<i>Cryptopipo holochlora</i>	73.5 \pm 1.06	46.5 \pm 0.99	3.9 \pm 0.11	7.1 \pm 0.14	16.1 \pm 0.49	10

Table 4.4 Sex-specific morphological measurements \pm their standard error. Sample sizes used for each sex are indicated below species names. Wing chord, tail length, bill length, and bill depth were measured in millimeters; body mass is in grams. Differences between measurements were determined using MANOVA where * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Species	Measurement	Males		Females		p-value
		Mean \pm SE	Range	Mean \pm SE	Range	
<i>Pipra fasciicauda</i> ♂ = 18 ♀ = 56	Wing chord	64.8 \pm 0.51	58–67	63.5 \pm 0.22	60–66	**
	Tail length	30.2 \pm 0.72	26–39	30.2 \pm 0.35	23–36	
	Bill width	4.0 \pm 0.08	3.5–4.9	4.2 \pm 0.05	3.4–5.1	*
	Bill length	7.3 \pm 0.17	5.8–8.9	7.4 \pm 0.07	6.2–8.6	
	Body mass	16.6 \pm 0.17	14.8–17.6	17.2 \pm 0.13	15.1–19.7	*
<i>Ceratopipra chloromeros</i> ♂ = 32 ♀ = 68	Wing chord	60.7 \pm 0.29	58–67	61.1 \pm 0.23	54–68	
	Tail length	25.7 \pm 0.31	21–31	27.1 \pm 0.26	21–36	**
	Bill width	4.0 \pm 0.08	2.8–5.3	4.3 \pm 0.05	3.4–5.5	**
	Bill length	6.6 \pm 0.10	5.5–7.7	7.0 \pm 0.06	5.2–8.5	***
	Body mass	16.4 \pm 0.17	14.9–19.2	17.2 \pm 0.14	14.8–19.8	**
<i>Lepidothrix coronata</i> ♂ = 27 ♀ = 64	Wing chord	58.4 \pm 0.26	55–61	56.7 \pm 0.23	51–62	***
	Tail length	28.4 \pm 0.23	26–30	28.1 \pm 0.20	23–32	
	Bill width	3.5 \pm 0.08	2.8–4.6	3.8 \pm 0.05	2.6–5.0	***
	Bill length	5.7 \pm 0.07	5.0–6.5	6.4 \pm 0.07	4.4–7.9	***
	Body mass	8.3 \pm 0.13	7.4–10.6	10.3 \pm 0.09	8.7–11.9	***
<i>Chiroxiphia boliviana</i> ♂ = 16 ♀ = 26	Wing chord	68.4 \pm 0.45	66–72	66.5 \pm 0.37	64–72	**
	Tail length	44.6 \pm 0.53	41–49	43.7 \pm 0.40	39–49	
	Bill width	3.7 \pm 0.09	2.9–4.1	3.9 \pm 0.09	2.9–4.5	
	Bill length	5.4 \pm 0.09	4.8–5.8	5.8 \pm 0.06	5.4–6.6	***
	Body mass	16.4 \pm 0.25	15.4–19.1	17.9 \pm 0.19	15.6–19.5	***

Table 4.5 Morphological measurements and associated standard errors (SE) for formative (FCF) and definitive plumage (DCB)

Manakins. Sample sizes for each age class are indicated below species names. Measurements are in mm except for mass (measured in grams). Difference between measurements were determined using MANOVA where * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Species	Measurement	FCF		DCB		p-value
		Mean \pm SE	Range	Mean \pm SE	Range	
<i>Pipra fasciicauda</i> FCF = 25 DCB = 75	Wing chord	62.9 \pm 0.31	60–67	63.8 \pm 0.21	58–67	*
	Tail length	31.8 \pm 0.61	26–41	30.2 \pm 0.30	23–39	*
	Bill width	4.1 \pm 0.1	2.7–5.5	4.2 \pm 0.05	3.4–5.1	
	Bill length	7.2 \pm 0.14	5.8–9.0	7.3 \pm 0.07	5.8–8.9	
	Body mass	16.1 \pm 0.19	14.6–18.4	17.0 \pm 0.11	14.8–19.7	***
<i>Ceratopipra chloromeros</i> FCF = 36 DCB = 106	Wing chord	62.1 \pm 0.24	60–65	61.0 \pm 0.18	54–68	**
	Tail length	28.1 \pm 0.28	25–33	26.7 \pm 0.26	21–36	***
	Bill width	4.3 \pm 0.10	3.4–6.0	4.2 \pm 0.05	2.8–5.5	
	Bill length	7.0 \pm 0.08	6.1–8.2	6.9 \pm 0.06	5.2–8.5	
	Body mass	16.1 \pm 0.15	14.5–18.7	16.9 \pm 0.16	14.8–19.8	***
<i>Lepidothrix coronata</i> FCF = 43 DCB = 93	Wing chord	56.8 \pm 0.25	52–60	57.2 \pm 0.20	51–62	
	Tail length	28.9 \pm 0.23	25–32	28.1 \pm 0.18	22–32	**
	Bill width	3.7 \pm 0.06	2.7–4.4	3.2 \pm 0.05	2.6–5.0	
	Bill length	6.2 \pm 0.11	5.0–8.6	6.7 \pm 0.07	4.4–7.9	
	Body mass	9.2 \pm 0.11	7.9–10.8	9.7 \pm 0.12	7.4–11.9	*
<i>Chiroxiphia boliviana</i> FCF = 24 DCB = 42	Wing chord	64.7 \pm 0.45	62–69	67.2 \pm 0.30	64–72	***
	Tail length	42.3 \pm 0.53	39–47	44.2 \pm 0.31	39–49	***
	Bill width	3.9 \pm 0.09	3.2–4.6	3.9 \pm 0.06	2.9–4.7	
	Bill length	5.7 \pm 0.09	5.0–6.2	5.7 \pm 0.06	4.8–6.6	
	Body mass	17.2 \pm 0.25	15.6–19.3	17.4 \pm 0.18	15.4–19.5	

Figure 4.1 Examples of the extent of preformative molt in tropical passerines where shaded feathers indicate replacement (adapted from Pyle 1997b). Many birds display a partial replacement pattern which includes lesser, median, and a variable number of greater coverts and tertial (a–b), while others have an incomplete pattern, replacing all of these tracks as well as some secondaries and primaries (c–d). Complete preformative molts (not shown) include all wing feathers.

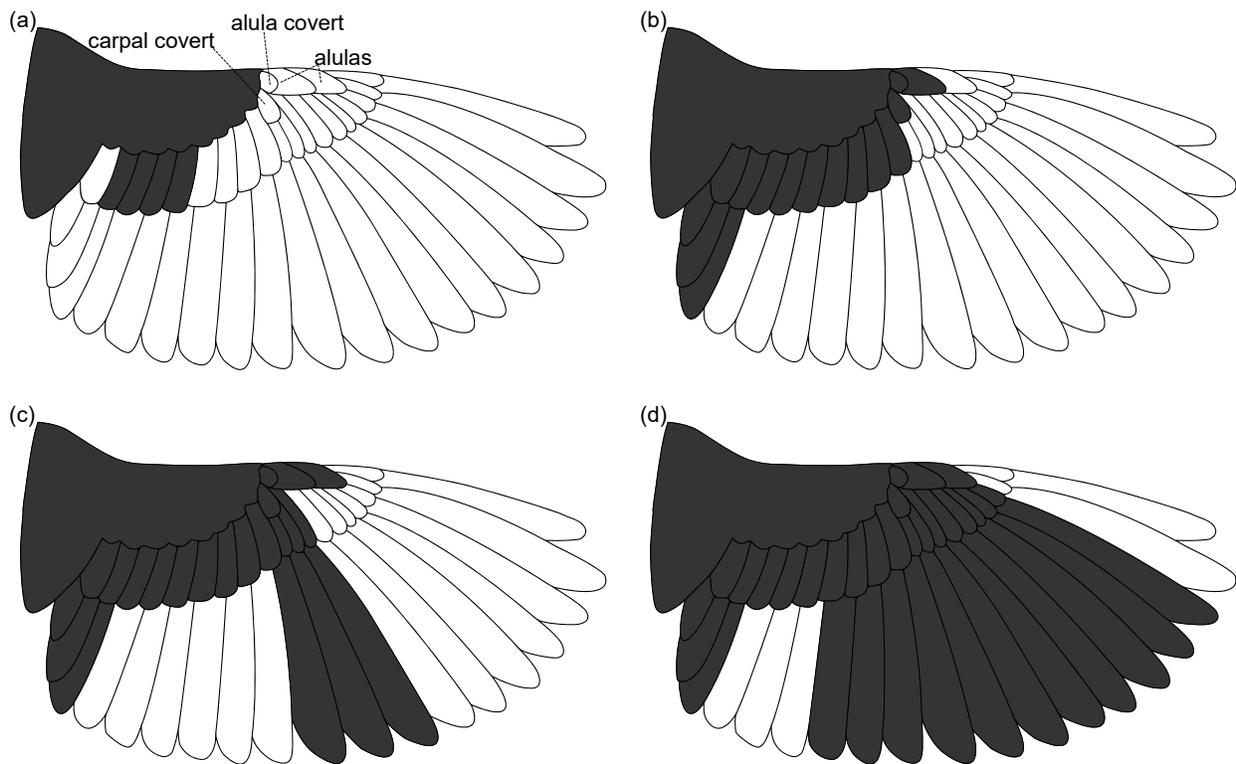


Figure 4.2 Patterns of feather replacement resulting from the preformative molt in seven manakin species (Pipridae). Gray scale indicates the frequency of observed feather replacement; darker shading indicates more frequent replacement.

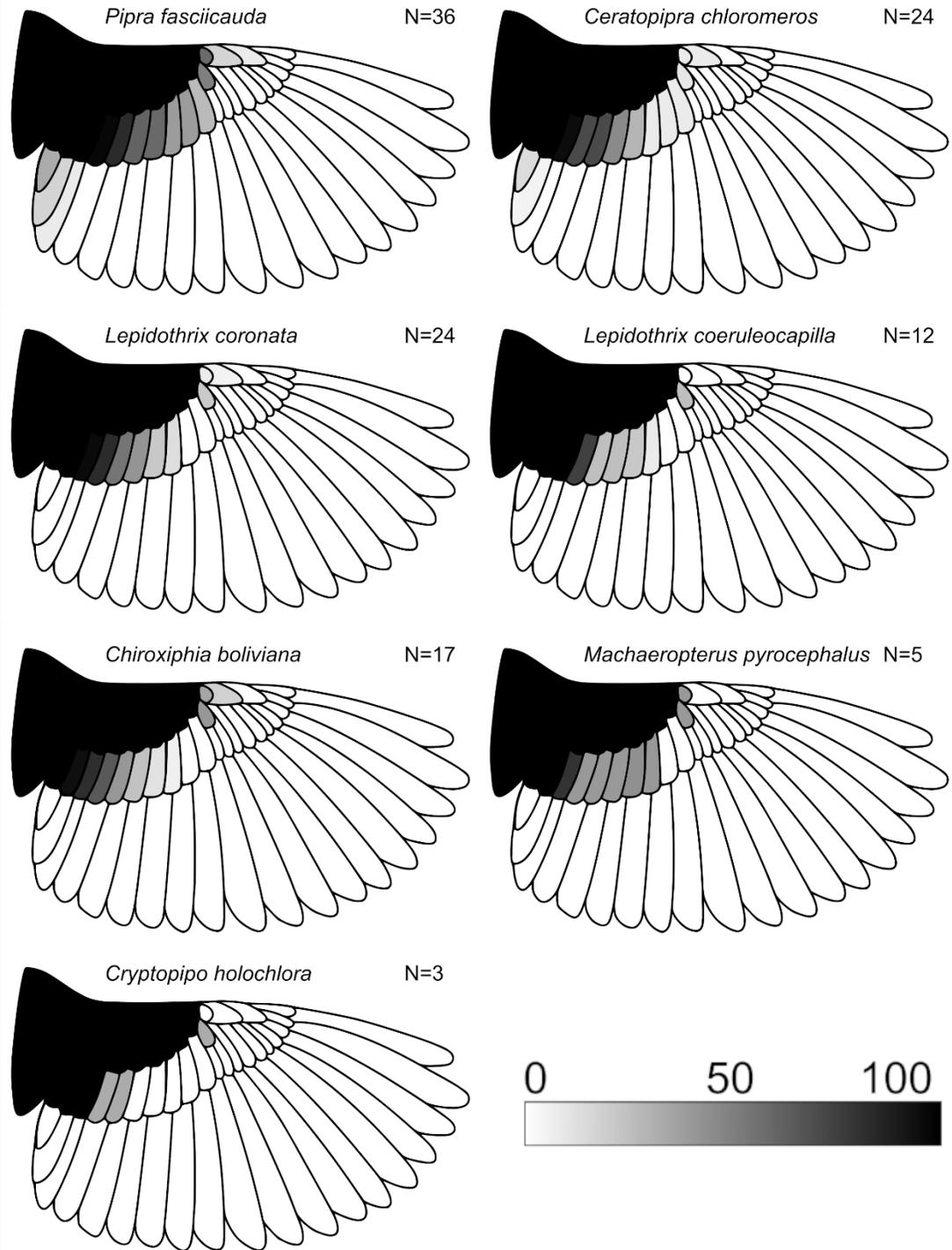


Figure 4.3 Male Band-tailed Manakins pass through a series of progressively more mature plumages. Shown here are birds in formative plumage (a) with a molt limit in the greater coverts (black arrow), second-cycle basic plumage (b) and definitive basic plumage (c), the latter two both lack molt limits. Formative plumage females appear similar to (a). Adult females achieve definitive plumage after the second molt cycle (d), and have uniform olive-green plumage. Some older birds obtain male-like plumage such as scattered red feathers on the crown and / or white inner webbing on the flight feathers, shown by the black arrow (e).



Figure 4.4 Formative plumage Round-tailed Manakin (a) with molt limit in the greater coverts (b), indicated by black arrow. Definitive plumage males (b–c) have uniform all black bodies and wings, with a red head and yellow thighs. Definitive plumage females have a characteristic dark eye, often with white flecking, occasionally, trace amounts of red feathers in the crown (black arrow in d), and uniform olive-green plumage overall.

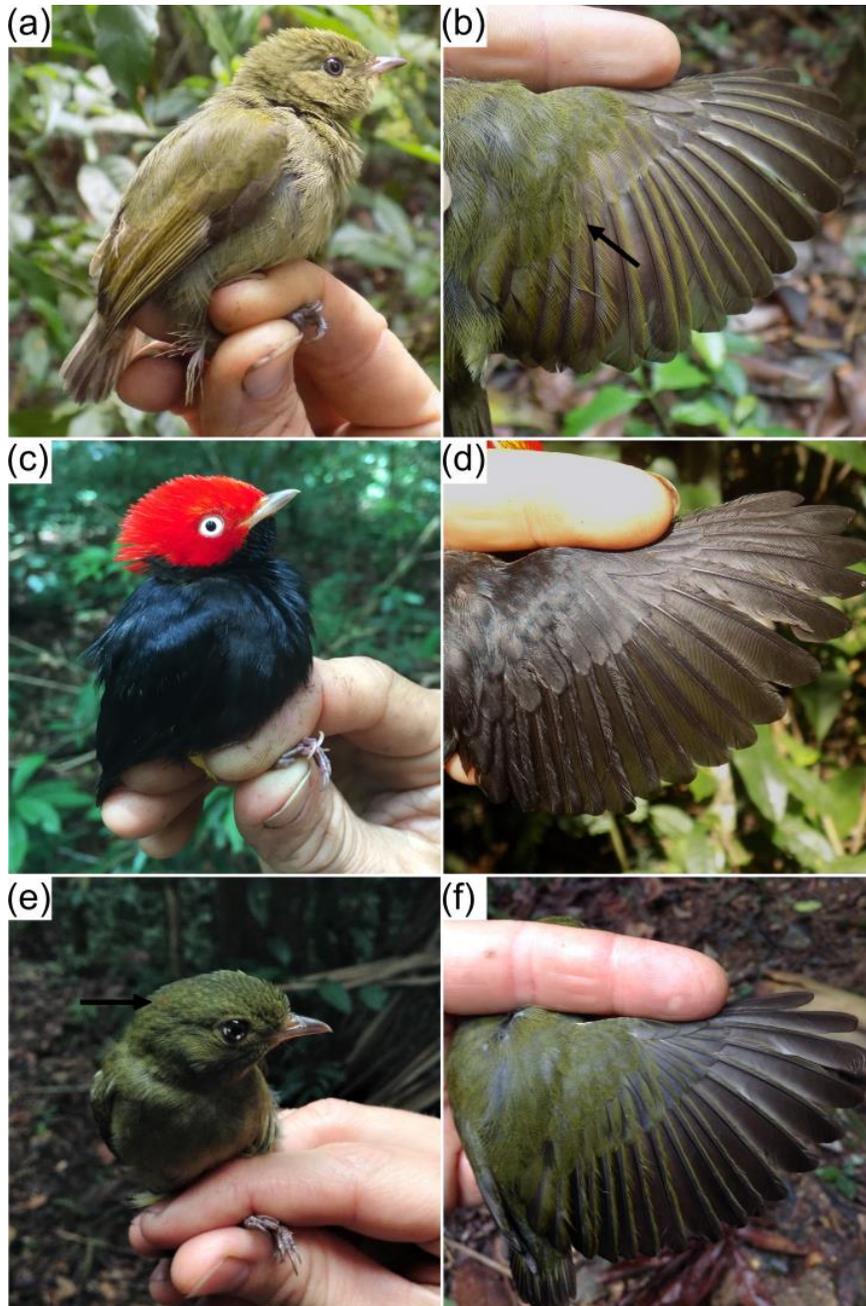


Figure 4.5 Formative plumage Blue-crowned Manakin (a) with molt limit in the greater coverts (b), indicated by black arrow. Definitive plumage males (c–d) have a blue crown, sooty face, reddish-brown eye, and uniform coverts with bright green edging. Adult females appear similar to FCF birds, but lack molt limits in the wing.

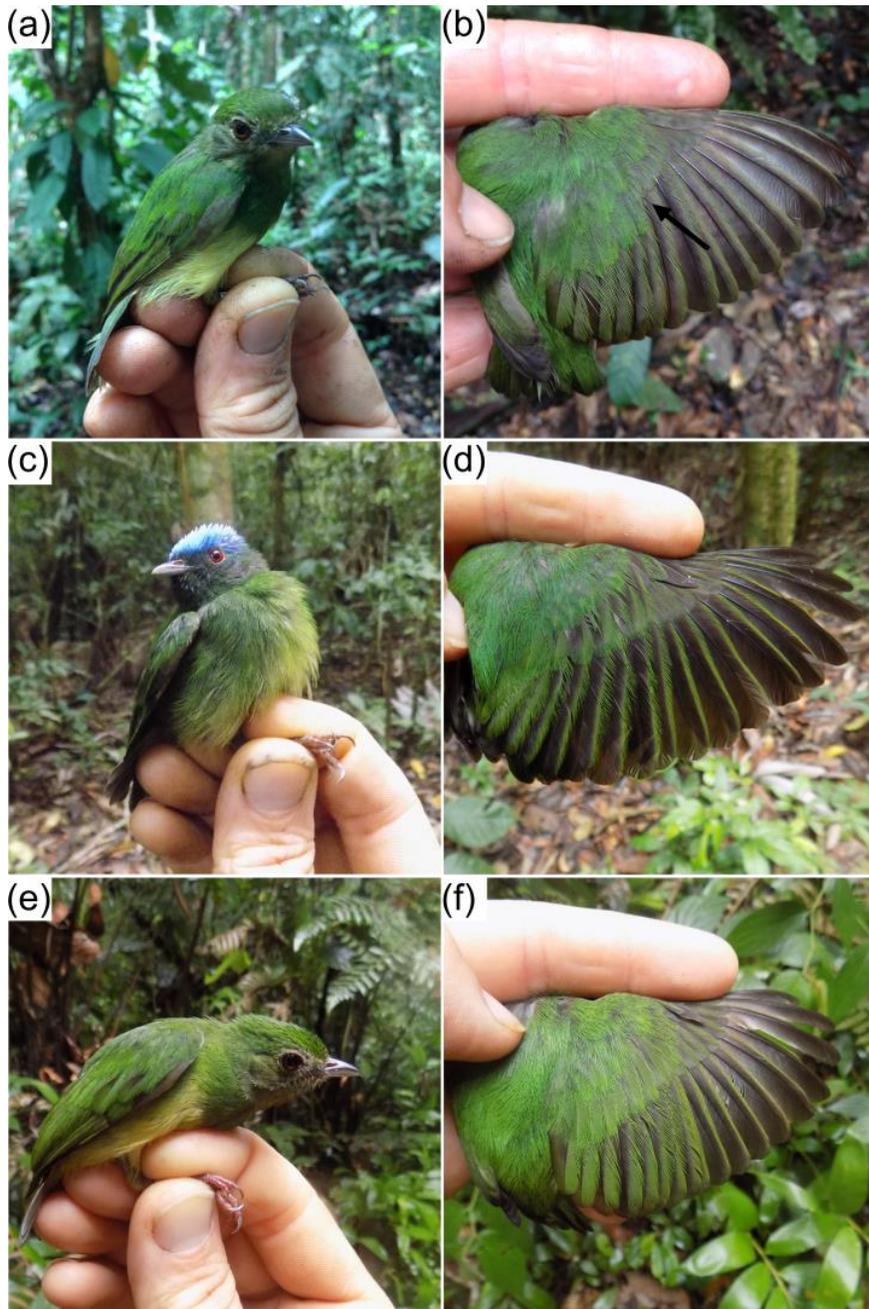


Figure 4.6 Formative plumage Cerulean-capped Manakin (a) with molt limit in the greater coverts (black arrow in b). Definitive plumage males (c–d) have uniform black bodies and wings, with an electric blue crown and rump. Some individuals retain greenish edging on coverts and flights feathers and can be aged as second-cycle basic (e). Adult females are all green and often have trace amounts of blue in the crown (black arrow in f) and rump and lack molt limits (g)

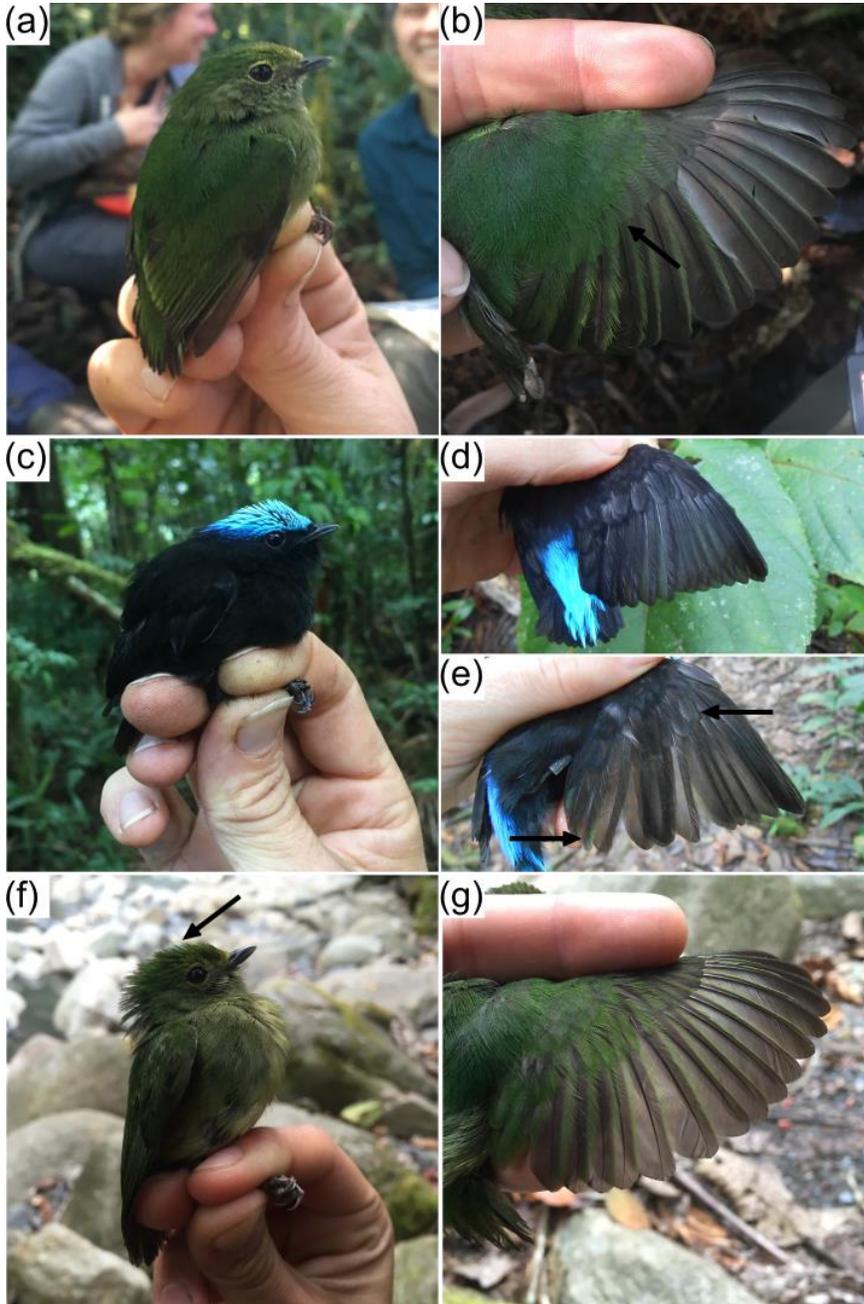


Figure 4.7 Male Yungas Manakins have three distinct plumages while females attain definitive plumage after the preformative molt. Shown here are males in formative plumage (a) with a molt limit in the greater coverts (black arrow), second-cycle basic plumage (b) and definitive basic plumage (c). Definitive plumage females appear similar to FCF birds (d), and have uniform olive-green plumage. Older birds occasionally obtain male-like plumage such as iridescent blue edging on covert and flight feathers.

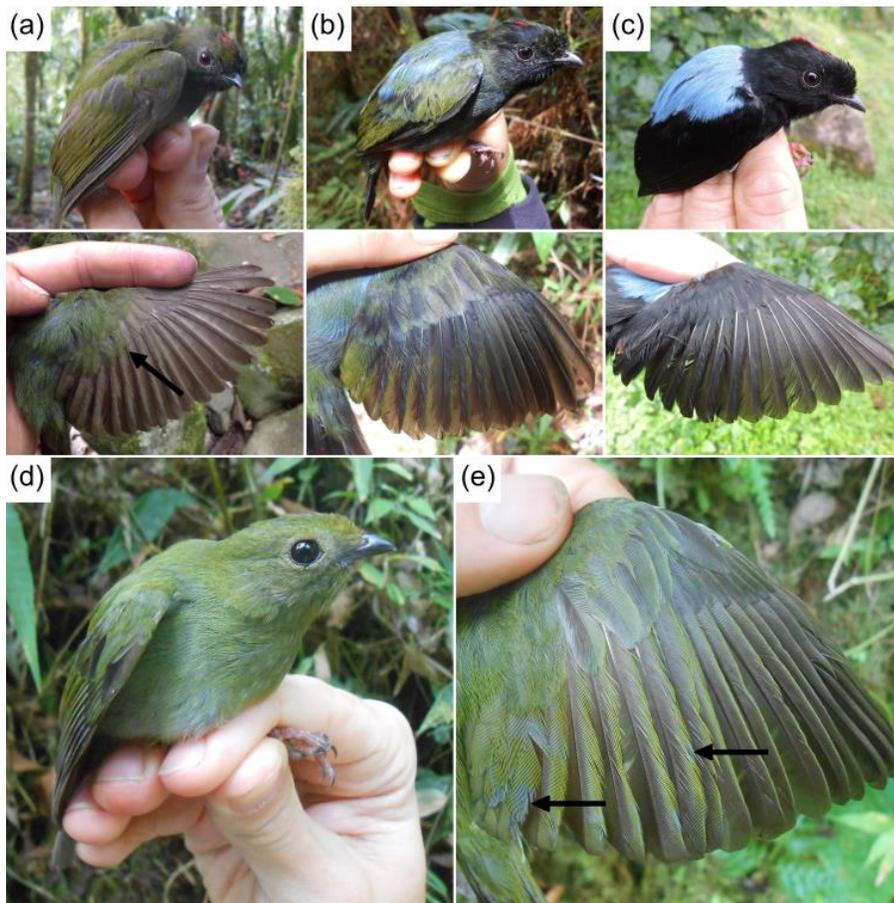


Figure 4.8 Formative plumage Fiery-capped Manakin (a) with molt limit in the greater coverts (b), indicated by black arrow. Definitive plumage males have a yellow crown with a red stripe, rose-brown back, pinkish streaking underneath, and a red eye (c). Wings are olive green transitioning distally to black with a grayish patch in inner secondaries. Definitive plumage females (e) lack molt limits (f), and may acquire brown on their back and rump (g).

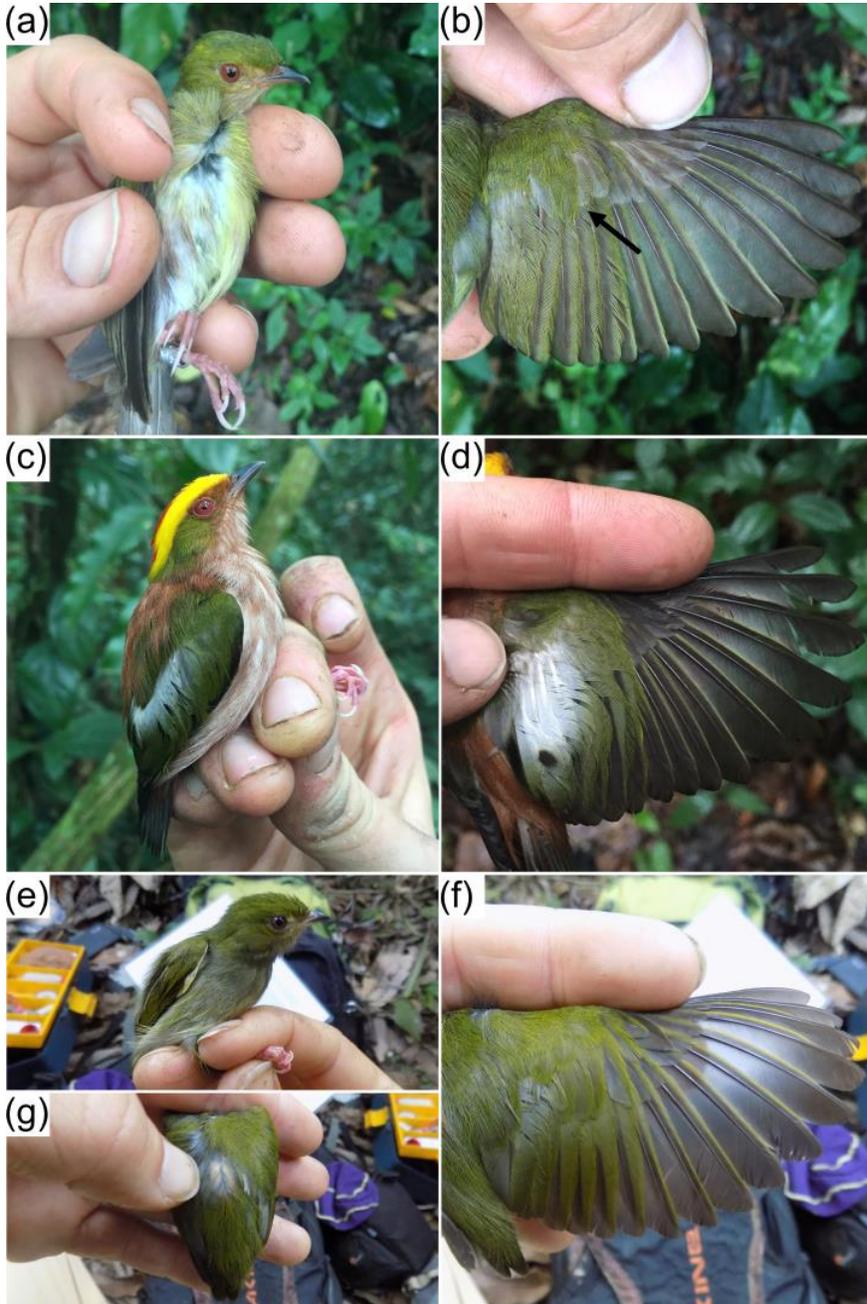


Figure 4.9 Formative plumage Green Manakin (a) with molt limit in the greater coverts (b), indicated by black arrow. Green Manakins have monochromatic definitive cycle plumage and both sexes appear all green (c), and lack molt limits in the greater coverts (d).



Chapter 5: General discussion

5.1 Dissertation overview

A main goal of my dissertation was to test pivotal allocation trade-offs and physiological constraints of survival rates predicted under a general theoretical framework, life history theory (LHT). My research has focused on tropical birds, which are known for their ‘slower’ life histories relative to temperate species (Wiersma et al. 2007b). My approach has been to integrate macroecological and physiological processes with comparative methods to address longstanding questions regarding the ultimate and proximate mechanisms associated with avian lifespan. I have drawn inspiration from large-scale biogeographical patterns, such as the latitudinal gradient in avian survival (Karr et al. 1990) and basal metabolic rate (BMR; Londoño *et al.* 2015), and used correlative methods to explore their ecological underpinnings. A second goal of my dissertation was to develop practical tools for improving survival estimation for field biologists. I accomplished this by considering variation in stage-specific survival rates, and outlining criteria that can be used to distinguish between age classes of tropical birds. This method can be applied by field-based researchers to produce refined estimates of survival.

5.2 Key findings

5.2.1 Life history and environmental correlates of survival

In Chapter 2, I synthesized research findings from 249 publications to examine patterns of covariation between survival and latitude worldwide. This is the most comprehensive analysis of avian survival rates to date, consisting of 1,007 estimates from 681 species in 58 countries. I demonstrate that, overall, an inverse relationship exists for northern hemisphere avifauna, but in

the southern hemisphere, only South American birds showed signs of higher survival with decreasing latitude while other biogeographical regions in the southern hemisphere showed no association between survival and latitude. These patterns are consistent with the observation that the latitudinal gradient in clutch size is also dampened in the southern hemisphere, specifically in the Afrotropics (Yom-Tov et al. 1994, Martin 1996, Evans et al. 2005), thus lending strong support to a survival–reproduction trade-off (Stearns 1989). This finding also suggests that hemispheric asymmetries in climatic conditions may lead to different evolutionary trajectories for species living at northern versus southern latitudes. And yet, most studies examining covariation of life history traits with latitude are based on the assumption of ecological equivalence between hemispheres (Chown et al. 2004). By accounting for these hemispheric differences, my study offers new insights into the interactions between climatic factors associated with latitude, life history traits, and lineage-specific effects, which have generated the diversity of life history strategies observed across our planet. I go on to show that body mass and clutch size are traits that strongly modulate these effects. Together these results illustrate the value of including intrinsic traits for understanding geographic patterns in demographic rates and suggest that avian survival is best accounted for by a combination of species' body size (i.e., body mass), reproductive output (i.e., clutch size), and latitude.

A suggested linkage between the higher survival of tropical birds is their lower metabolic rates — data show that tropical birds have lower BMR compared to temperate species (Ricklefs and Wikelski 2002, Wiersma et al. 2007a, Williams et al. 2010, Londoño et al. 2015). Lower rates of energy metabolism may reduce the amount of oxidative damage accumulated during aerobic respiration (Vágási et al. 2019), prolonging overall lifespan. Although functional mechanisms, such as smaller organ masses and increased antioxidant properties of cells, have

been proposed to explain lower BMR in tropical species (Williams et al. 2010), the assumption that lower BMR translates into higher survival has remained largely untested. In Chapter 3, I showed that BMR is negatively correlated with apparent survival across 37 species of tropical birds, providing strong evidence for the link between metabolism and lifespan. Additionally, I showed that bird species living at higher montane elevations appeared to have lower survival than lowland birds. Thus, tropical montane species may be anomalous with respect to the slow-fast continuum of life histories, given metabolic rates similar to lowland species, but lower survival rates. If true, this suggests that no suite of life history characteristics is optimal for coping with the harsher climate conditions at high elevations, or from an evolutionary perspective, that montane species are still adapting to local climatic conditions. This is the first study to demonstrate empirical support for an inverse relationship between survival and BMR measured from the same populations of free-living organisms. For the majority of species in this study, this work is also the first to produce estimates of their survival rates, thereby providing a foundation for future studies of demographic characteristics of Neotropical birds from this region.

5.2.2 Molt limits as a tool for aging birds and improving estimates of survival

Significant differences exist between survival rates and reproductive success of young versus old individuals, as well as between males versus females (Martin 1995a, Payevsky et al. 1997, Székely et al. 2014). Yet information regarding differences in plumage and, in the case of monochromatic species, morphometric measurements, to distinguish between stage-specific classes is lacking for most species outside of North America and Europe. In Chapter 4, I demonstrate how knowledge of molt patterns and their resulting plumages can be applied to age

tropical birds. I showed that, like temperate species, the majority of birds from South America replace only a portion of the wing feathers following the first prebasic molt (i.e., the first molt following acquisition of juvenile plumage). This partial preformative molt facilitates separation of birds into discrete age classes, which can then be modeled using a capture-mark-recapture (CMR) framework. This has the potential to improve model precision by accounting for heterogeneous recapture rates among birds of varying ages.

5.3 Challenges of working with survival rates

Survival rates are inherently difficult to study in free-living populations of animals because they require the initial capture and subsequent recapture, resighting, or recovery of marked individuals throughout their lifetime. This dilemma is exacerbated in long-lived and / or wide-ranging organisms, such as many species of birds considered in this dissertation. Thus, successfully quantifying trends in avian survival requires long-term monitoring of up to a decade or more (Ruiz-Guitérrez et al. 2012). The capacity of different regions and governments to support such ventures varies greatly throughout the world. Lack of knowledge of survival rates is therefore often a logistical problem, both temporally and spatially. Temporal constraints often manifest themselves as low precision in survival estimates (Sandercock 2006, Blake and Loiselle 2013), while spatial constraints limit our ability to generalize observations over the great diversity of avian life histories found worldwide. These issues are particularly prevalent in tropical regions, where data collection is geographically sparse, and often is collected over shorter intervals compared with the temperate zone.

One way that I attempted to overcome these challenges was by integrating results of survival analyses from many different studies (Chapter 2). This meta-analytical approach had the

advantage of allowing me to address a global-scale question that would have been logistically infeasible to accomplish otherwise, as well as increase the statistical power of my models. Even so, small sample size may have limited my ability to detect differences between survival and latitude in some groups, such as nonpasserines, where 85% of effect sizes came from latitudes above 35° compared to only 15% from the tropics and 27% from austral locations. Furthermore, while the range of species and sites included in my global analysis is valuable for explaining broad-scale geographical patterns, it may also have obscured my ability to detect differences across latitudes or between data subsets, since in some cases the advantages of one life-history strategy in a particular location may not be successful in another. For instance, to be a nonmigratory owl has different implications in an African savannah vs. Arctic tundra. These potential limitations aside, the global patterns I identified are congruent with previous work that suggests that survival and latitude covary inversely (Peach et al. 2001, Muñoz et al. 2018), and that this relationship is strongly mediated by trade-offs between survival, clutch size, and body mass.

Finally, the patterns of variation in survival, environmental characteristics, and life history traits that I document in Chapters 2 and 3 are assumed to reflect data on adult birds of both sexes. However, criteria for defining an adult often differ between studies. For instance, in many tropical studies, a lack of information on differences in plumage between juveniles and adults leads researchers to employ times-since-marking (TSM) models. TSM models separate the first transition after capture from later intervals, the same as coding individuals into two age-classes (Sandercock 2006). In theory, estimates calculated over the first-time interval reflect juvenile survival, while estimates made over the second- and later-time intervals are used to represent adult survival. The underlying assumption here is that juveniles are more likely to be

transient while adults are sedentary. But data show that adult floaters (i.e., nonbreeders) often makeup a variable amount of the population (Penteriani et al. 2011). A more effective means of estimating survival would be to model age-classes directly. In some cases, researchers may have been unable to distinguish between juveniles and adults due to lack of information regarding how to separate age classes. This is particularly true for tropical studies. Indeed, there were no tropical studies I encountered where stage-specific age classes were used to model survival. In the case of my work in Chapter 3, for instance, I was unable to apply age classes as a covariate because two of the six years of data collection lacked this information. It was this lack of information that inspired me to develop sexing and aging criteria for a number of species from my study area in southeastern Peru (e.g., Kennedy *et al.* 2018, Chapter 4 of this dissertation). Despite the inherent drawbacks in using survival rates derived from CMR studies, these estimates remain the best data currently available for this key life-history trait.

5.4 Future directions

My results from Chapter 2 demonstrate the existence of a latitudinal gradient in survival for passerines in the northern hemisphere, and for New World birds in general for the southern hemisphere. However, my literature search was not exhaustive, and there remain substantial gaps in the spatial coverage of my models, particularly from North and Central Africa and much of the Indomalayan and Australasian biogeographical realms. As many as 3,700 species are found throughout Asia alone — more than a third of the world’s avifauna. Some of these regions contain lineages of birds that have evolved under very different ecological circumstances, and thus may be expected to deviate from the patterns I generally observed. For instance, many temperate-breeding Australian birds display a suite of slow life-history characteristics (i.e., high

survival and small clutch size), but these traits are not accompanied by low BMR (Bech et al. 2016). A focus on survival estimates from these regions is therefore needed to achieve a coherent picture of global variation in survival. Figure 2.1 provides a roadmap to identifying data deficient areas around the globe where we know very little about avian survival and its intrinsic and extrinsic correlates.

Many countries have regional or nation-wide banding programs capable of producing estimates of survival rates, but the data remain unavailable, unanalyzed, or both. In part, our ability to bridge macroecological and evolutionary processes to describe life history variation has languished because of a lack of data accessibility. A laudable goal, therefore, is for banding programs throughout the world to work towards making these data more readily available (e.g., following the MAPS banding database model) and to better equip researchers with the ability to analyze data for marked populations of birds.

Another research avenue that deserves additional attention is the relationship between survival and other measures of energy metabolism. Birds rarely experience conditions under which BMR is measured (i.e., nonmolting, nonbreeding, fasted individuals measured during their sleep phase, and in thermally neutral conditions), but BMR has been a staple for comparison because of the relative ease with which it can be measured in the laboratory and the field, and because it provides an integrated view of the maintenance energy requirements of an individual associated with its ecological conditions (Daan et al. 1990). A more direct measure linking survival and lifespan to an organism's daily energy expenditure could be obtained using field metabolic rate (FMR). Several methods have been applied to study FMR in live birds, such as using doubly labelled water (DLW), which is based on differences in the elimination rate of isotopes of oxygen and hydrogen from body water as a function of carbon dioxide (Speakman

and Hambly 2016). Recent advancements that use oral dosing to deliver isotopic tracers and subsequent faecal sampling to assess the initial and final oxygen / hydrogen ratios offer a feasible? non-invasive sampling alternative for application in the field (Bourne et al. 2019). By pairing data from color-banded birds to generate survival estimates while also facilitating identification of individuals for DLW treatment, this approach would provide a strong validation of the negative relationship between energy metabolism and survival suggested by my work.

The relationships outlined in this dissertation between survival rates, intrinsic life history traits, and extrinsic ecological factors have been tested across latitudes and elevational gradients within the temperate region. Studies that assess these relationships across tropical montane ecosystems are, however, especially under-represented (Boyle et al. 2016). Indeed, I was unable to locate any information on survival rates for anything other than tropical lowland species as part of my literature review in Chapter 2. Montane birds are widely projected to decline or disappear completely due to upslope range shifts associated with climate change (Şekercioğlu et al. 2008, Laurance et al. 2011, Freeman et al. 2018). My results from Chapter 3 illustrate that tropical montane species may be characterized by a unique suite of traits in their pace of life, in which BMR does not differ from lowland birds, but survival does. Consequently, montane species may experience different selective pressures (Boyle et al. 2016) or have unique population demographic responses in coping with future climate change. Understanding the life history traits shared by montane communities may therefore shed light into their sensitivity to climate change, and help to more effectively direct conservation initiatives.

Finally, I suggest that the life-history trade-offs and constraints I discuss in Chapters 2 and 3 be examined using stage-specific survival rates. Differences between males and females and between adult and juveniles regarding habitat use could help refine conservation efforts

tasked with species management (Morton 1990, Figuerola et al. 2001). Could a latitudinal survival gradient exist only for juveniles and be masked by data on adults when observations fail to account for age-classes? Recent work by Muñoz *et al.* (2018) on New World birds suggest this is likely not the case, but the idea is intriguing and additional research on Old World birds should be assessed to test this hypothesis. I did not account for stage-specific survival differences in Chapter 2, in part because no study provided separate estimates for juveniles versus adults from the tropics, and only nine of the 431 tropical estimates provided information for both males and females. Similarly, in Chapter 3, I only estimated adult survival using the TSM models described above, because only a portion of the birds included in the analysis were assigned to age and sex classes. Since variation in stage-specific survival can shape the evolution of life histories (Reznick et al. 1990, Martin 1995b), differences between survival rates of males and females, and juveniles and adults, is an important component of understanding life history strategies in general, and is critical for effective conservation management (Skalski et al. 2005).

5.5 Closing remarks

To conclude, I have used macroecological and comparative approaches combined with rigorous field data to test several predictions of LHT. I have demonstrated that a latitudinal survival gradient exists, but that survival is better predicted by trade-offs with two key life history variables: clutch size and body mass. I have also shown that energy metabolism predicted survival rates in 37 species of tropical birds, thus filling an important knowledge gap in LHT. Future researchers can refine these predictions by using stage-specific estimates of survival by separating birds into age classes based on patterns of molt and their resulting plumages. I hope that my research results will provide a platform for better understanding variation in survival

rates and their links to species intrinsic traits and the extrinsic factors that characterize their environment.

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Appendix A: Chapter 2 supplemental information

Chapter 2 Supplementary references Bibliographic information for the 249 studies used in the meta-analysis.

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Chapter 2 Supplementary methods Detailed description of the data compilation methods used in this study.

We first searched for studies based from bibliographies compiled from previous publications of avian survival (Newton et al. 2016, Méndez et al. 2018, Muñoz et al. 2018). We then searched online using combinations of the following terms: ‘survival’, ‘mortality’, ‘vital rate’, or ‘demography’, and ‘bird’ or ‘avian’ in the Web of Science Core Collections and on Google Scholar. Our initial survey resulted in over 2000 publications. We then screened titles and abstracts of publications and considered them for final inclusion in the meta-analysis if they met the following criteria: (1) the study provided estimates of adult survival, not juvenile or nestling, at the species level. (2) The species studied was not pelagic. (3) The study did not include harvested or captive-bred populations, whose survival rates may not reflect those experienced under natural conditions. (4) Survival rate was estimated on the breeding grounds (i.e., we did not include estimates from studies of over-wintering or migratory stopover sites). (5) The data were collected from marked populations of birds to estimate apparent or true survival using one of three methods: live-recovery / resight models, dead-recovery models, or more complex models that used a combination of these two approaches. (6) The study was conducted for at least 3 years, which is the minimum number of occasions needed to estimate the probability of encounter (p) from live-encounter data (Sandercock 2006). To avoid sex-biased differences in survival probability (Székely et al. 2014), we also required that (7) the estimate of survival included data from both males and females. In cases when studies had overlapping data, we retained the publication that presented the most information (i.e., had more precise estimates or used a larger dataset). This second review narrowed the window of appropriate publications to

319. However, many of these papers did not report measurement error on survival rate, which is required to weight individual effect sizes in meta-analyses. Our global dataset therefore consisted of 1007 effect sizes extracted from 249 publications. The majority of these effects (82%) came from passerine birds, and effect sizes obtained from the New World biogeographical realms (282 Nearctic and 298 Neotropical) were more numerous than those from Old World studies (177, 170, and 51 of effect sizes from the Palearctic, Afrotropical, and Indomalayan realms, respectively). Approximately twice as many estimates were available from studies conducted in the northern hemisphere ($n = 684$) compared to the southern hemisphere ($n = 323$). The majority of effect sizes reported per study was 1 (geometric mean = 1.6, $SD = 12.4$) and multiple estimates for the same species were available from different studies for 168 species, accounting for 49% of all effect sizes included in the analysis.

For each species in each study, we extracted relevant data on survival and latitude. For those studies lacking a well-defined location (i.e., broad-scale studies of survival spanning continents or countries) we used the R package *auk* to assign and estimate latitude. For each target region and species defined by the study, we extracted eBird observations submitted over the last 15 years during the breeding period (May 1–August 8 for birds from Canada, the United States, and Europe, and September 1–December 8 for species from South Africa). We further filtered data to include only complete eBird checklists (i.e. those where users specify that all species seen or heard are reported), which allowed us to identify implicit non-detections for each species, and by stationary counts <24 hours, traveling counts <25 km, and area counts within a circle of radius 25 km. We then overlaid the eBird checklists with a 25 km equal-area raster grid and calculated the frequency of occurrence of each species on checklists within each grid cell. We took a weighted average of the grid-cell centers, using the species observation frequency as

the weight, and used the geographic coordinates of this centroid to represent the species-site specific latitude.

Chapter 2 Supplementary tables Descriptive statistics and AIC_C model selection results from the variable selection procedure and meta-analysis.

Table A.1 Spearman rank correlations of variables considered for the meta-analysis of avian survival rates. Correlations ≥ 0.70 are highlighted in bold. Variable abbreviations are: *Precip* = annual precipitation in mm, *Temp*_{Winter} = minimum winter temperature, *Temp*_{Seasonality} = difference between mean temperature of the three warmest and three coldest months. *Nonmigrant* is a binary variable describing whether a species migrates or remains a resident throughout its annual cycle.

	<i>Latitude</i>	<i>Precip</i>	<i>Temp</i> _{Winter}	<i>Temp</i> _{Seasonality}	<i>Mass</i>	<i>Clutch size</i>	Nonmigrant
<i>Latitude</i>		-0.28	-0.63	0.64	0.10	0.57	-0.67
<i>Precip</i>	-0.28		0.71	-0.67	-0.10	-0.48	0.38
<i>Temp</i> _{Winter}	-0.63	0.71		-0.92	-0.13	-0.64	0.62
<i>Temp</i> _{Seasonality}	0.64	-0.67	-0.92		0.17	0.66	-0.66
<i>Body mass</i>	0.10	-0.10	-0.13	0.17		-0.12	-0.06
<i>Clutch size</i>	0.57	-0.48	-0.64	0.66	-0.12		-0.50
<i>Nonmigrant</i>	-0.67	0.38	0.62	-0.66	-0.06	-0.50	

Table A.2 Single-predictor meta-regression models of extrinsic and intrinsic moderators hypothesized to effect adult survival rates and ranked by AIC_C . See Table A.1 for variable abbreviations.

Model	K	AIC_C	ΔAIC_C
<i>Body mass</i>	5	1532.71	0.00
<i>Clutch size</i>	5	1535.52	2.81
<i>Latitude</i>	6	1592.47	59.76
<i>Temp_{Seasonality}</i>	5	1597.36	64.65
<i>Nonmigrant</i>	5	1598.38	65.66
<i>Temp_{Winter}</i>	5	1598.68	65.97
<i>Precip</i>	5	1606.39	73.68
Null	4	1613.66	80.95

Table A.3 Multi-predictor meta-regression models of either extrinsic climate factors or intrinsic traits. Models were developed by sequentially adding the best performing moderators until AIC was no longer improved. The Null model is included for comparison. See Table A.1 for variable abbreviations.

Model	<i>K</i>	AIC _C	Δ AIC _C
Null	4	1613.66	
Extrinsic climate factors			
<i>Temp</i> _{Seasonality} + <i>Precip</i>	6	1596.68	0.00
<i>Temp</i> _{Seasonality} + <i>Temp</i> _{Winter} + <i>Precip</i>	7	1596.97	0.29
<i>Temp</i> _{Seasonality} + <i>Temp</i> _{Winter}	6	1597.34	0.66
<i>Temp</i> _{Seasonality}	5	1597.36	0.68
Intrinsic traits			
<i>Body mass</i> + <i>Clutch size</i> + <i>Nonmigrant</i>	7	1450.04	0.00
<i>Body mass</i> + <i>Clutch size</i>	6	1456.73	6.69
<i>Body mass</i>	5	1532.71	82.67

Table A.4 Back-transformed mean-survival rates for each data subset, their upper and lower bound %95 confidence interval, the number effect sizes used in the analysis, and two measures of total heterogeneity: Cochran's Q and I^2 values.

Data used	Mean survival	95% CI lower	95% CI upper	No. effect sizes used	Cochran's Q	I^2
All data	0.67	0.48	0.83	1007	$P > 0.001$	0.98
Passerines	0.63	0.39	0.83	825	$P > 0.001$	0.96
Nonpasserines	0.69	0.49	0.84	182	$P > 0.001$	0.99
Old World	0.68	0.46	0.84	397	$P > 0.001$	0.97
New World	0.66	0.45	0.83	580	$P > 0.001$	0.95
Mainland	0.66	0.47	0.81	930	$P > 0.001$	0.98
Island	0.75	0.57	0.87	77	$P > 0.001$	0.92

Chapter 2 Supplementary figures Supporting figures showing phylogeny, results of the sensitivity analysis, and model fit.

Figure A.1 Phylogenetic relationships of the 681 species of birds used in the global meta-analysis of survival rates. Most species (82%) were in order Passeriformes. The call out shows non-passerine orders used in the analysis. Red circles indicate nodes demarking branches for each of the orders. Abbreviations are: Cl = Coliiformes, Co = Columbiformes, Gr = Gruiformes, Pe = Pelcaniformes. From clockwise from top right, asterisk symbols show orders represented by a single species: Psittaciformes, Caprimulgiformes, Cuculiformes, Ciconiformes.

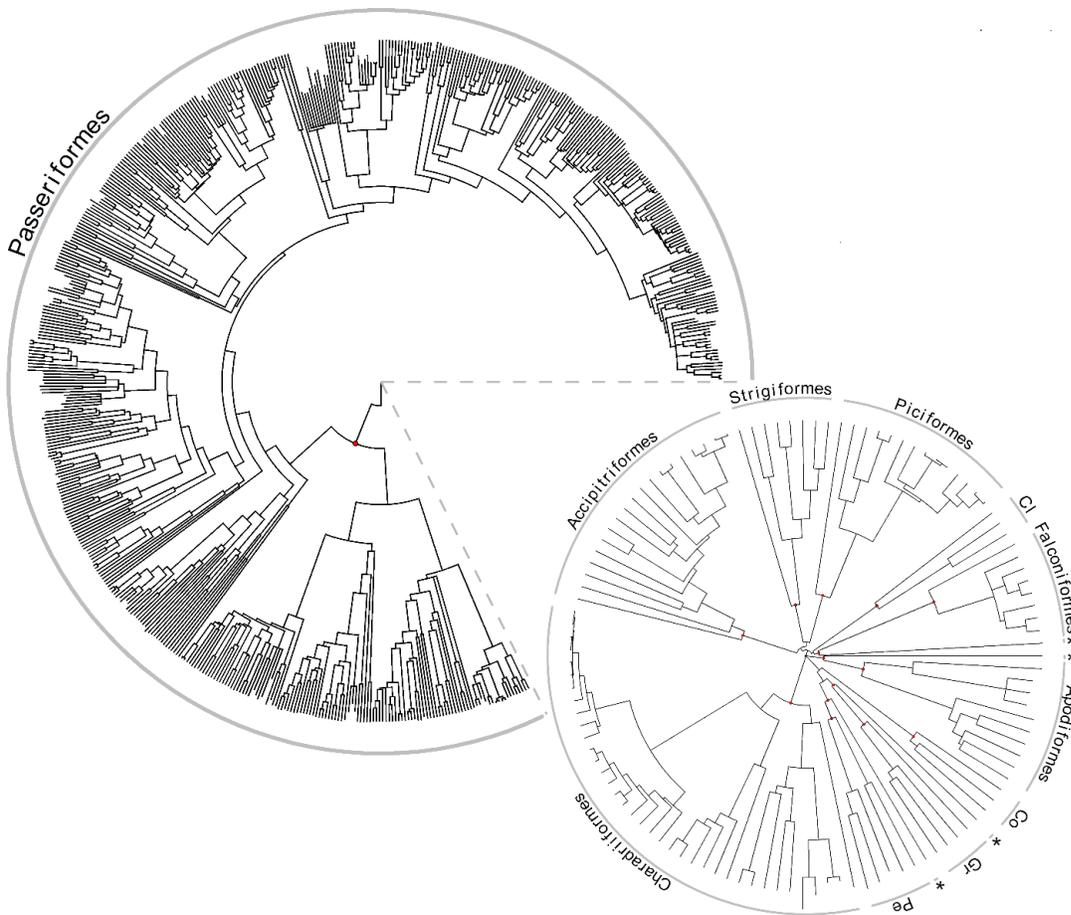


Figure A.2 Funnel plot used to evaluate publication bias for the global analysis of 1007 effect sizes plotted against their precision.

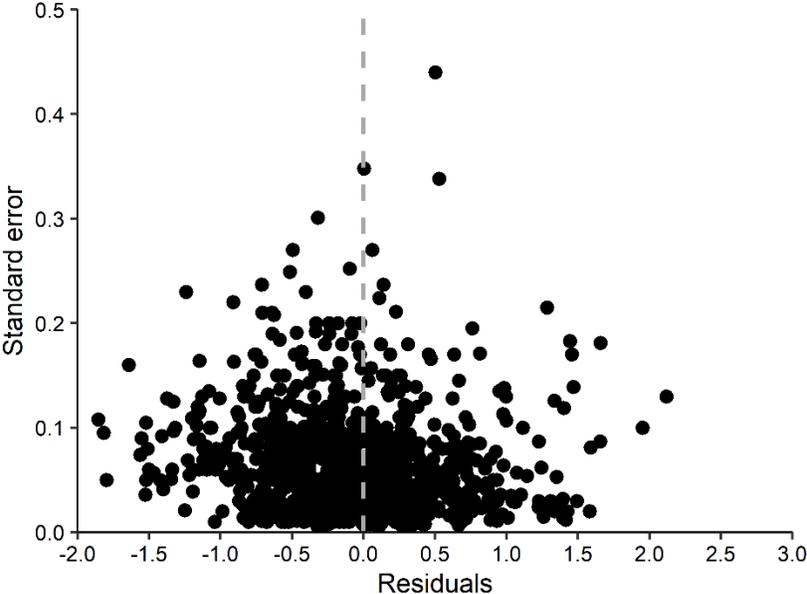


Figure A.3 Results of the sensitivity analysis comparing the meta-analytic mean of the entire dataset to a reduced dataset consisting of studies that reported ≤ 10 effect sizes (reduced model 1), a reduced dataset consisting of studies that collected data for ≥ 10 years (reduced model 2), effect size estimated separately for each of three methods used to estimate survival, and effect size calculated from studies where we used the package *auk* to approximate species' geographic coordinates compared to those studies where authors provided information on latitude and longitude. Bars represent 95% confidence limits. Dashed line indicates the overall meta-analytical mean.

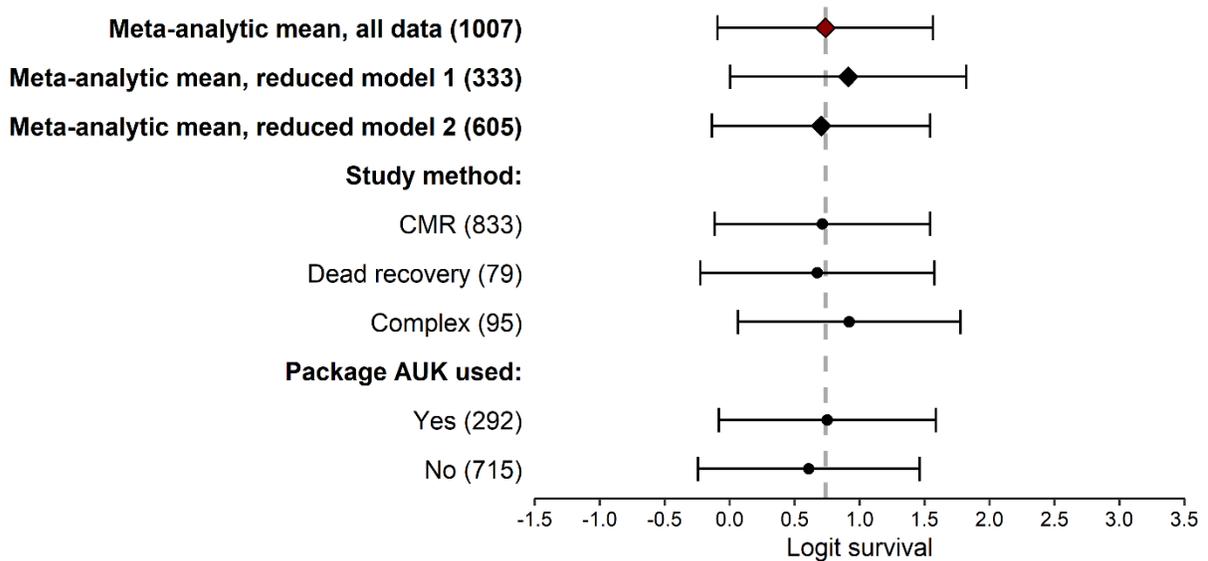
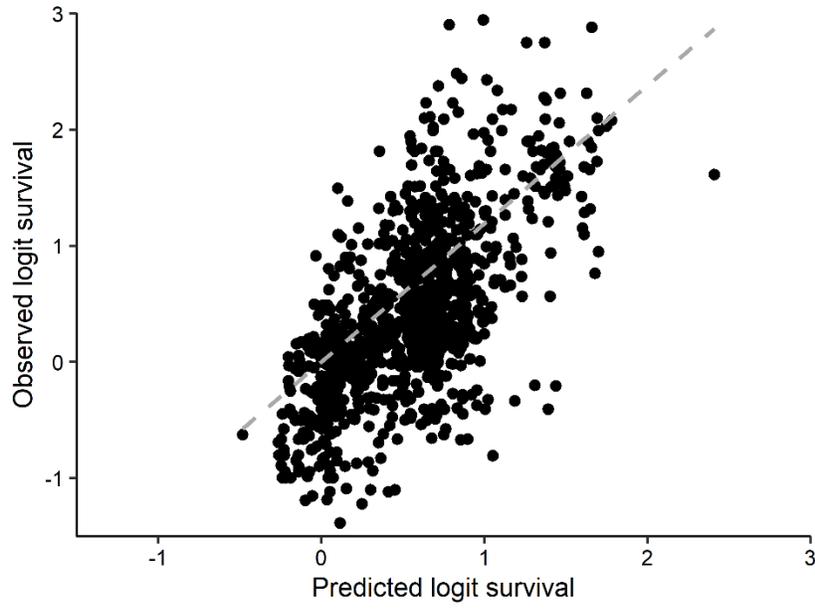


Figure A.4 Model fit for the observed survival rate and that predicted by the joint extrinsic / intrinsic model (Table 2.1) for an assemblage of 681 species of birds across the globe.



Appendix B: Chapter 3 supplemental information

Chapter 3 Supplementary methods Collection and calculation of basal metabolic rate and an assessment of its seasonal variation.

Measurements were taken from birds captured in the afternoon as part of the current study between 2011 and 2013. Birds were marked and processed as described above and held overnight to measure BMR using open-circuit respirometry if they met the following criteria: 1) were nonreproductive (i.e., had no brood patch or cloaca protuberance), 2) had no active molt of flight feathers, remiges, or >10% body feathers, and 3) were no longer in juvenile plumage and therefore assumed to be independent of parental care. Data were excluded for birds that were not quiescent during measurements or had body temperatures above their thermoneutral zone (<35 °C). Measurements for BMR were taken at least five hours after capture to assure individuals were post-adsorbed (i.e., were not expending energy on digestion). BMR was calculated as the the lowest continuous average $\dot{V}O_2$ (mL O₂ min⁻¹) over 5 min during periods when $\dot{V}O_2$ was low and stable and birds had been at constant ambient temperature for at least 1 h. Birds were tested at both 30 and at 32–34 °C and the lowest of the two metabolic rates as BMR was used. The mean $\dot{V}O_2$ per species (mean number of individuals sampled = 13.2; range = 1–41) was converted to watts using a coefficient of 19.8 Joules mL⁻¹ O₂ (Gessaman and Nagy 1988).

To examine seasonal variation in BMR we used a linear mixed effects model to account for hierarchically structured data, such as observations within sites within years, conducted with the *R* package *lme4* (Bates et al. 2015). We defined three broad seasons for our study area based on Rapp & Silman (2012): dry (June–July), transitional (August–September), and wet (October–November). Because not all species were sampled in more than one season, we first subset our

data to include those species with >10 samples collected in three or more months. We first included the variables *season*, *species*, and their interaction term as fixed effects in the model and *year* and *site* as random effects. Using a likelihood-ratio test, we compared model fit between this full model to a reduced model where only *species* was included as a fixed effect (Table B.2). We found little support that season influenced BMR and thus did not include sampling date as a potential nuisance parameter in our analysis (Figures B.1 and B.2).

Chapter 3 Supplementary tables Sampling effort, AIC model selection results, and survival estimates and predictor variables calculated for 37 species of tropical birds from Peru.

Table B.1 Approximate number of net hours per plot for each of the three stations operated in the Manu Biosphere Reserve, Peru, from 2011–2016. Station and annual totals are given in bold.

Plot name	Year					
	2011	2012	2013	2014	2015	2016
Pantiacolla: 21,161	2,412	4,201	4,036	4,196	4,321	1,995
capybara1	248	440	453	407	411	255
capybara2	233	428	388	380	492	225
miles	246	417	425	475	307	195
mirador	241	420	403	390	463	199
monksaki1	275	387	400	405	415	202
monksaki2	213	428	384	330	494	229
monksaki3	224	365	457	445	458	195
monksaki4	252	454	413	413	357	195
ranacocha	217	472	400	490	462	135
tinamou	263	390	313	461	462	165
San Pedro: 21,089	2,402	3,935	4,099	4,096	4,489	2,068
kitchen1	240	409	396	401	470	194
kitchen2	247	360	440	431	468	219
loop1	280	392	370	272	525	230
loop2	217	392	419	378	530	234
lucho1	240	350	420	460	455	197
lucho2	251	350	410	488	486	202
river1	229	430	408	441	374	232
river2	228	442	418	475	430	198
river3	235	428	403	542	359	215
river4	235	382	415	208	392	147
Wayqecha: 17,871		3,820	3,869	3,676	4,509	1,997
canopy1		450	420	381	459	199
canopy2		415	398	416	484	218
oso1		375	389	345	477	195
oso2		365	323	363	379	185
oso3		340	324	379	436	194
oso4		345	407	352	435	195
oso5		385	413	360	414	213
oso6		415	415	372	464	213
oso7		390	400	348	488	190
zorro		340	380	360	473	195

Table B.2 Results of the likelihood-ratio test used for comparing goodness of fit between the full and reduced mixed effects models exploring seasonal variation in basal metabolic rate. The full model included *species*, *season* (dry, transitional, or wet) and their interaction term as fixed effects while the reduced model only included *species* as a predictor. Evaluation statistics are Akaike's Information Criterion corrected for small sample size (AIC_C), difference in AIC_C (ΔAIC_C), model deviance, chi square (χ^2) statistic, and whether the addition of *season* improved model fit (p-value).

Model	AIC_C	ΔAIC_C	Deviance	χ^2	p-value
Reduced	-5.44	0.00	-23.44		
Full	4.12	9.23	-35.88	12.44	0.33

Table B.3 Range in the duration of time intervals between sampling (in years) used to adjust CJS models for the three research stations in sampled in the Manu Biosphere Reserve, Peru.

Station	Year					
	2011	2012	2013	2014	2015	2016
Pantiacolla	0.68	0.70	0.70	0.80	0.83	0.68
San Pedro	0.67	0.71	0.70	0.80	0.81	0.67
Wayqecha	0.66	0.70	0.87	0.75	0.84	0.66

Table B.4 Description and notation for candidate Cormack-Jolly-Seber models used to estimate apparent annual survival for 37 species of Neotropical passerine birds captured between 2011 and 2016 in the Manu Biosphere Reserve, southeastern Peru. Model notation includes parameters for survival (ϕ) and probability of recapture (p). For 10 species, we were unable to fit fully time dependent recapture probability (see Table S5). The number of species for which an associated model was selected based on QAIC_C and likelihood ratio tests is indicated by No. selected.

Model notation	No. selected	Model interpretation
$\phi(.) p(.)$	25	Constant survival (ϕ) and constant recapture probability (p)
$\phi(.) p(t)$	5	Constant survival (ϕ) and time-dependent recapture (p)
$\phi(2./.) p(.)$	5	Time since marking model with two classes of survival, constant survival during the first year ϕ^1 and subsequent years ϕ^2 , and constant recapture (p)
$\phi(2./.) p(t)$	2	Time since marking model with two classes of survival, constant survival during the first year ϕ^1 and subsequent years ϕ^2 , and time-dependent recapture (p)

Table B.5 Results of goodness-of-fit testing (\hat{c}) for apparent annual survival of 37 Neotropical bird species from the Manu Biosphere Reserve with varying model assumptions of constancy of survival (ϕ) and recapture rates (p). Evaluation statistics are number of parameters (k), Quasi-Akaike's Information Criterion corrected for small sample size (QAIC_C) and adjusted for overdispersion, change in QAIC_C from the top model (Δ QAIC_C), relative strength of support for selected model (w_i), and model deviance. The top model selected for each species based on QAIC and likelihood-ratio tests is in bold.

Species	\hat{c}	K	Model†	QAIC _C	Δ QAIC _C	w_i	Deviance
Thamnophilidae							
<i>Thamnomanes ardesiacus</i>	1.80	3	$\phi(\cdot)p(\cdot)$	66.64	0.00	0.71	13.37
		4	$\phi(2./.)p(\cdot)$	68.54	1.90	0.27	13.10
		7	$\phi(\cdot)p(t)$	74.85	8.21	0.01	12.64
		8	$\phi(2./.)p(t)$	76.84	10.20	0.00	12.27
<i>Isleria hauxwelli</i>	1.68	3	$\phi(\cdot)p(\cdot)$	93.17	0.00	0.56	24.02
		4	$\phi(2./.)p(\cdot)$	94.02	0.85	0.36	22.72
		7	$\phi(\cdot)p(t)$	98.23	5.07	0.04	20.27
		8	$\phi(2./.)p(t)$	98.61	5.44	0.04	18.34
<i>Oneillornis salvini</i>	1.51	7	$\phi(\cdot)p(t)$	85.57	0.00	0.47	11.39
		3	$\phi(\cdot)p(\cdot)$	86.63	1.06	0.28	21.57
		8	$\phi(2./.)p(t)$	87.84	2.27	0.15	11.24
		4	$\phi(2./.)p(\cdot)$	88.58	3.01	0.10	21.32
<i>Willisornis poecilinotus</i>	1.87	3	$\phi(\cdot)p(\cdot)$	46.91	0.00	0.69	10.52
		4	$\phi(2./.)p(\cdot)$	48.66	1.75	0.29	10.00
		7	$\phi(\cdot)p(t)$	54.13	7.22	0.02	8.20
		8	$\phi(2./.)p(t)$	56.01	9.10	0.01	7.48

Species	\hat{c}	K	Model†	QAIC _C	Δ QAIC _C	w_i	Deviance
Furnariidae							
<i>Dendrocincla fuliginosa</i>	1.44	3	$\varphi(\cdot)p(\cdot)$	63.24	0.00	0.76	21.36
		4	$\varphi(2./.)p(\cdot)$	65.66	2.42	0.23	21.34
		7	$\varphi(\cdot)p(t)$	72.45	9.21	0.01	19.98
		8	$\varphi(2./.)p(t)$	74.72	11.48	0.00	19.22
<i>Dendrocincla merula</i>	1.68	3	$\varphi(\cdot)p(\cdot)$	58.75	0.00	0.64	15.59
		4	$\varphi(2./.)p(\cdot)$	60.17	1.42	0.31	14.67
		7	$\varphi(\cdot)p(t)$	64.75	6.00	0.03	11.59
		8	$\varphi(2./.)p(t)$	66.63	7.88	0.01	10.68
<i>Glyphorhynchus spirurus</i>	1.14	4	$\varphi(2./.)p(\cdot)$	428.54	0.00	0.66	39.00
		3	$\varphi(\cdot)p(\cdot)$	429.99	1.45	0.32	42.50
		8	$\varphi(2./.)p(t)$	435.79	7.24	0.02	37.90
		7	$\varphi(\cdot)p(t)$	436.98	8.44	0.01	41.20
<i>Xiphorhynchus elegans</i>	1.77	3	$\varphi(\cdot)p(\cdot)$	68.51	0.00	0.69	17.71
		4	$\varphi(2./.)p(\cdot)$	70.18	1.66	0.30	17.11
		7	$\varphi(\cdot)p(t)$	76.73	8.22	0.01	16.41
		8	$\varphi(2./.)p(t)$	78.62	10.11	0.00	15.71
<i>Xenops minutus</i>	1.53	3	$\varphi(\cdot)p(\cdot)$	57.52	0.00	0.68	14.19
		4	$\varphi(2./.)p(\cdot)$	59.02	1.51	0.32	13.28
		7	$\varphi(\cdot)p(t)$	67.62	10.10	0.00	13.85
		8	$\varphi(2./.)p(t)$	69.65	12.13	0.00	12.91
<i>Anabacerthia striaticollis</i>	1.59	3	$\varphi(\cdot)p(\cdot)$	81.27	0.00	0.62	18.52
		4	$\varphi(2./.)p(\cdot)$	83.49	2.22	0.20	18.52
<i>Thripadectes melanorhynchus</i>	1.35	3	$\varphi(\cdot)p(\cdot)$	104.92	0.00	0.71	17.27
		4	$\varphi(2./.)p(\cdot)$	106.95	2.03	0.26	17.09
		7	$\varphi(\cdot)p(t)$	111.62	6.70	0.02	14.77
		8	$\varphi(2./.)p(t)$	113.84	8.92	0.01	14.53

Species	\hat{c}	K	Model†	QAIC _C	Δ QAIC _C	w_i	Deviance
<i>Premnoplex brunnescens</i>	1.36	3	$\phi(\cdot)p(\cdot)$	136.21	0.00	0.72	20.85
		4	$\phi(2./.)p(\cdot)$	138.28	2.07	0.26	20.81
		7	$\phi(\cdot)p(t)$	143.69	7.49	0.02	19.66
		8	$\phi(2./.)p(t)$	145.96	9.75	0.01	19.66
Tyrannidae							
<i>Mionectes striaticollis</i>	1.26	8	$\phi(2./.)p(t)$	146.76	0.00	0.89	8.02
		7	$\phi(\cdot)p(t)$	151.00	4.24	0.11	14.36
		4	$\phi(2./.)p(\cdot)$	157.29	10.53	0.00	26.89
		3	$\phi(\cdot)p(\cdot)$	160.36	13.60	0.00	32.01
<i>Mionectes olivaceus</i>	1.40	7	$\phi(\cdot)p(t)$	144.27	0.00	0.38	16.10
		3	$\phi(\cdot)p(\cdot)$	144.39	0.11	0.36	24.75
		4	$\phi(2./.)p(\cdot)$	146.40	2.13	0.13	24.68
		8	$\phi(2./.)p(t)$	146.44	2.17	0.13	16.05
<i>Mionectes oleagineus</i>	1.89	4	$\phi(2./.)p(\cdot)$	176.59	0.00	0.56	21.95
		3	$\phi(\cdot)p(\cdot)$	177.45	0.87	0.36	24.89
		8	$\phi(2./.)pi(t)$	181.40	4.82	0.05	18.30
		7	$\phi(\cdot)p(t)$	182.60	6.01	0.03	21.64
<i>Leptopogon amaurocephalus</i>	0.95	4	$\phi(2./.)p(\cdot)$	80.76	0.00	0.77	24.65
		3	$\phi(\cdot)p(\cdot)$	83.16	2.40	0.23	29.37
<i>Leptopogon superciliaris</i>	2.35	3	$\phi(\cdot)p(\cdot)$	41.71	0.00	0.72	10.07
		4	$\phi(2./.)p(\cdot)$	43.72	2.01	0.26	9.79
		7	$\phi(\cdot)p(t)$	49.36	7.65	0.02	8.03
		8	$\phi(2./.)p(t)$	51.82	10.11	0.00	7.84
<i>Ochthoeca pulchella</i>	0.79	6	$\phi(\cdot)p(t)$	191.31	0.00	0.60	8.47
		7	$\phi(2./.)p(t)$	193.45	2.14	0.21	8.42
		3	$\phi(\cdot)p(\cdot)$	194.21	2.90	0.14	17.73
		4	$\phi(2./.)p(\cdot)$	196.22	4.91	0.05	17.65

Species	\hat{c}	K	Model†	QAIC _C	Δ QAIC _C	w_i	Deviance
Pipridae							
<i>Chiroxiphia boliviana</i>	1.01	3	$\phi(\cdot)p(\cdot)$	155.05	0.00	0.68	29.50
		4	$\phi(2./.)p(\cdot)$	156.52	1.47	0.32	28.85
<i>Lepidothrix coronata</i>	1.58	7	$\phi(\cdot)p(t)$	303.86	0.00	0.72	30.33
		8	$\phi(2./.)p(t)$	305.88	2.02	0.26	30.23
		3	$\phi(\cdot)p(\cdot)$	312.87	9.01	0.01	47.64
		4	$\phi(2./.)p(\cdot)$	314.70	10.84	0.00	47.42
<i>Lepidothrix coeruleocapilla</i>	1.43	3	$\phi(\cdot)p(\cdot)$	88.30	0.00	0.57	21.79
		4	$\phi(2./.)p(\cdot)$	88.89	0.59	0.43	20.13
<i>Pipra fasciicauda</i>	1.01	8	$\phi(2./.)p(t)$	348.46	0.00	0.96	24.14
		7	$\phi(\cdot)p(t)$	355.41	6.95	0.03	33.21
		4	$\phi(2./.)p(\cdot)$	358.85	10.38	0.01	42.90
		3	$\phi(\cdot)p(\cdot)$	362.03	13.57	0.00	48.14
<i>Ceratopipra chloromeros</i>	1.79	3	$\phi(\cdot)p(\cdot)$	67.82	0.00	0.69	17.51
		4	$\phi(2./.)p(\cdot)$	69.49	1.67	0.30	16.91
		7	$\phi(\cdot)p(t)$	76.05	8.23	0.01	16.23
		8	$\phi(2./.)p(t)$	77.95	10.13	0.00	15.54
Troglodytidae							
<i>Cinnycerthia fulva</i>	1.06	3	$\phi(\cdot)p(\cdot)$	154.04	0.00	0.52	17.42
		6	$\phi(\cdot)p(t)$	155.78	1.74	0.22	12.53
		4	$\phi(2./.)p(\cdot)$	155.93	1.89	0.20	17.15
		7	$\phi(2./.)p(t)$	158.08	4.04	0.07	12.53
<i>Cyphorhinus thoracicus</i>	1.52	3	$\phi(\cdot)p(\cdot)$	57.37	0.00	0.75	13.61
		4	$\phi(2./.)p(\cdot)$	59.57	2.20	0.25	13.48
Turdidae							
<i>Catharus dryas</i>	0.99	3	$\phi(\cdot)p(\cdot)$	84.56	0.00	0.65	29.17
		4	$\phi(2./.)p(\cdot)$	85.84	1.27	0.35	28.04
<i>Turdus albicollis</i>	1.68	3	$\phi(\cdot)p(\cdot)$	57.94	0.00	0.76	17.29
		4	$\phi(2./.)p(\cdot)$	60.25	2.31	0.24	17.29

Species	\hat{c}	K	Model†	QAIC _C	Δ QAIC _C	w_i	Deviance
Thraupidae							
<i>Diglossa cyanea</i>	2.26	4	$\phi(2./.)p(.)$	147.48	0.00	0.64	20.71
		3	$\phi(.)p(.)$	148.96	1.48	0.30	24.26
		7	$\phi(2./.)p(t)$	152.94	5.47	0.04	19.84
		6	$\phi(.)p(t)$	154.41	6.94	0.02	23.44
<i>Kleinotherapis atropileus</i>	2.15	3	$\phi(.)p(.)$	45.09	0.00	0.64	9.90
		4	$\phi(2./.)p(.)$	46.72	1.63	0.29	9.29
		6	$\phi(.)p(t)$	50.28	5.19	0.05	8.18
		7	$\phi(2./.)p(t)$	51.79	6.70	0.02	7.25
<i>Sphenopsis melanotis</i>	1.01	4	$\phi(2./.)p(.)$	75.78	0.00	0.78	22.54
		3	$\phi(.)p(.)$	78.25	2.48	0.22	27.27
<i>Iridosornis jelskii</i>	0.79	3	$\phi(.)p(.)$	67.76	0.00	0.36	11.12
		4	$\phi(2./.)p(.)$	68.12	0.35	0.30	9.11
		6	$\phi(.)p(t)$	68.84	1.08	0.21	4.80
		7	$\phi(2./.)p(t)$	69.62	1.86	0.14	2.88
<i>Chlorospingus flavigularis</i>	1.70	3	$\phi(.)p(.)$	73.58	0.00	0.70	20.16
		4	$\phi(2./.)p(.)$	75.66	2.08	0.25	20.00
		7	$\phi(.)p(t)$	79.55	5.97	0.04	16.78
		8	$\phi(2./.)p(t)$	81.40	7.83	0.01	16.11
Emberizidae							
<i>Atlapetes melanolaemus</i>	1.16	6	$\phi(.)p(t)$	288.60	0.00	0.46	18.71
		7	$\phi(2./.)p(t)$	288.96	0.36	0.39	16.96
		3	$\phi(.)p(.)$	291.99	3.38	0.09	28.29
		4	$\phi(2./.)p(.)$	292.63	4.03	0.06	26.88
Parulidae							
<i>Myiothlypis signata</i>	1.04	4	$\phi(2./.)p(.)$	62.27	0.00	0.52	18.72
		3	$\phi(.)p(.)$	63.06	0.79	0.35	21.97
<i>Myiothlypis bivittata</i>	1.44	3	$\phi(.)p(.)$	50.33	0.00	0.72	12.07
		4	$\phi(2./.)p(.)$	52.51	2.18	0.24	11.85

Species	\hat{c}	K	Model†	QAIC _C	ΔQAIC _C	w_i	Deviance
<i>Myiothlypis luteoviridis</i>	0.64	6	$\phi(\cdot)p(t)$	173.84	0.00	0.69	5.94
		7	$\phi(2./.)p(t)$	175.53	1.69	0.30	5.40
		3	$\phi(\cdot)p(\cdot)$	183.30	9.46	0.01	21.87
		4	$\phi(2./.)p(\cdot)$	184.78	10.94	0.00	21.22
Fringillidae							
<i>Euphonia xanthogaster</i>	1.54	3	$\phi(\cdot)p(\cdot)$	65.85	0.00	0.54	18.25
		4	$\phi(2./.)p(\cdot)$	66.21	0.36	0.46	16.38

† Key to model notation is $\phi(\cdot)p(\cdot)$, constant survival and recapture across all years; $\Phi(\cdot)p(t)$, constant survival and year specific recapture probability; $\phi(2./.)p(\cdot)$, Time-since-marking model (TSM; Cooch and White 2005) with constant recapture and two classes of survival allowing for the effect of transients or young birds; $\phi(2./.)p(t)$, TSM model with year specific recapture.

Table B.6 Results of the univariate ordinary least squares analysis comparing three models of elevation: continuous (mean capture elevation), categorical (Pantiacolla, San Pedro, Wayqecha), or binary (lowland < 1000 m, versus montane > 1000 m).

Independent variable	Elevation model	AIC	df	Adjusted R^2
Survival	Binary	105.30	1	0.09
	Categorical	106.69	2	0.08
	Continuous	108.42	1	0.01
BMR	Continuous	109.50	2	-0.02
	Binary	111.23	1	-0.03
	Categorical	109.90	1	-0.03

Table B.7 Sample sizes, predictor variables, and survival estimates with associated standard errors for 37 species of tropical birds from the Manu Biosphere Reserve, southeastern Peru. Basal metabolic rate (BMR) from Londoño et al. (2015). Elevation was calculated as the mean elevation where each species was captured. Transient survival (ϕ^1) was estimated for species that included time since marking in the top model based on QAIC_C and likelihood ratio tests. Resident survival (ϕ^{+2}) was included in all models.

Species	No. individuals captured	No. recaptures	No. individuals recaptured	Mass (g)	BMR (watts)	Elevation (m)	ϕ^1	SE	ϕ^{+2}	SE
Thamnophilidae										
<i>Thamnomanes ardesiacus</i>	92	26	12	17.91	0.30	413	-	-	0.57	0.23
<i>Isleria hauxwelli</i>	107	37	16	11.28	0.21	420	-	-	0.56	0.19
<i>Oneillornis salvini</i>	75	34	15	26.14	0.32	437	-	-	0.50	0.16
<i>Willisornis poecilinotus</i>	59	20	10	18.24	0.39	460	-	-	0.53	0.25
Furnariidae										
<i>Dendrocincla merula</i>	36	30	11	48.74	0.62	426	-	-	0.41	0.13
<i>Dendrocincla fuliginosa</i>	28	27	11	31.77	0.37	432	-	-	0.50	0.15
<i>Glyphorhynchus spirurus</i>	246	155	64	15.51	0.25	443	0.28	0.04	0.47	0.08
<i>Xiphorhynchus elegans</i>	56	32	32	40.54	0.51	438	-	-	0.51	0.15
<i>Xenops minutus</i>	35	25	25	12.17	0.18	427	-	-	0.61	0.20
<i>Anabacerthia striaticollis</i>	70	38	38	24.91	0.35	1431	-	-	0.50	0.16
<i>Thripadectes melanorhynchus</i>	63	26	20	46.12	0.54	1363	-	-	0.41	0.10
<i>Premnoplex brunnescens</i>	94	58	26	16.04	0.32	1384	-	-	0.48	0.10
Tyrannidae										
<i>Mionectes striaticollis</i>	325	44	20	14.61	0.26	1485	0.12	0.08	0.54	0.23
<i>Mionectes olivaceus</i>	112	64	28	14.92	0.28	1286	-	-	0.45	0.08
<i>Mionectes oleagineus</i>	196	99	42	11.52	0.18	427	0.21	0.07	0.46	0.11
<i>Leptopogon amaurocephalus</i>	50	21	10	11.94	0.22	433	0.15	0.08	0.68	0.29
<i>Leptopogon superciliaris</i>	58	27	12	13.21	0.25	1386	-	-	0.38	0.18
<i>Ochthoeca pulchella</i>	118	59	27	12.41	0.17	2617	-	-	0.51	0.12

Species	No. individuals captured	No. recaptures	No. individuals recaptured	Mass (g)	BMR (watts)	Elevation (m)	ϕ^1	SE	ϕ^{+2}	SE
Pipridae										
<i>Chiroxiphia boliviana</i>	124	41	19	17.23	0.30	1421	-	-	0.39	0.16
<i>Lepidothrix coronata</i>	215	156	68	9.86	0.20	439	-	-	0.69	0.10
<i>Lepidothrix coeruleocapilla</i>	51	43	16	10.57	0.24	1379	-	-	0.50	0.10
<i>Pipra fasciicauda</i>	190	105	42	16.86	0.26	416	0.27	0.06	0.72	0.14
<i>Ceratopipra chloromeros</i>	216	76	35	16.87	0.29	424	-	-	0.51	0.16
Troglodytidae										
<i>Cinnycerthia fulva</i>	86	53	24	17.62	0.20	2729	-	-	0.50	0.11
<i>Cyphorhinus thoracicus</i>	45	26	12	31.82	0.42	1357	-	-	0.34	0.11
Turdidae										
<i>Catharus dryas</i>	35	24	10	36.92	0.46	1335	-	-	0.58	0.15
<i>Turdus albicollis</i>	48	24	11	50.60	0.46	419	-	-	0.54	0.24
Thraupidae										
<i>Diglossa cyanea</i>	226	37	17	18.53	0.32	2775	0.13	0.08	0.60	0.24
<i>Kleinothraupis atropileus</i>	62	23	23	20.57	0.38	2761	-	-	0.35	0.18
<i>Sphenopsis melanotis</i>	69	17	10	18.35	0.19	1497	0.12	0.07	0.70	0.34
<i>Iridosornis jelskii</i>	43	20	10	20.48	0.38	2787	-	-	0.40	0.16
<i>Chlorospingus flavigularis</i>	56	36	15	26.01	0.33	1363	-	-	0.43	0.13
Emberizidae										
<i>Atlapetes melanolaemus</i>	221	98	43	26.46	0.34	2648	-	-	0.62	0.12
Parulidae										
<i>Myiothlypis signata</i>	35	19	10	13.49	0.22	2661	-	-	0.39	0.14
<i>Myiothlypis bivittata</i>	38	19	11	15.04	0.30	1347	-	-	0.34	0.16
<i>Myiothlypis luteoviridis</i>	119	53	25	14.81	0.23	2721	-	-	0.60	0.12
Fringillidae										
<i>Euphonia xanthogaster</i>	101	40	16	14.01	0.22	1293	-	-	0.37	0.11

Chapter 3 Supplementary figures Seasonal variation in basal metabolic rate, phylogenetic relationships, and previously published survival estimates for select species also used in this study.

Figure B.1 Monthly estimates of basal metabolic rate (BMR) for six species of tropical birds from southeastern Peru. A linear model fit is plotted as a dashed line with shaded 95% confidence intervals for each species.

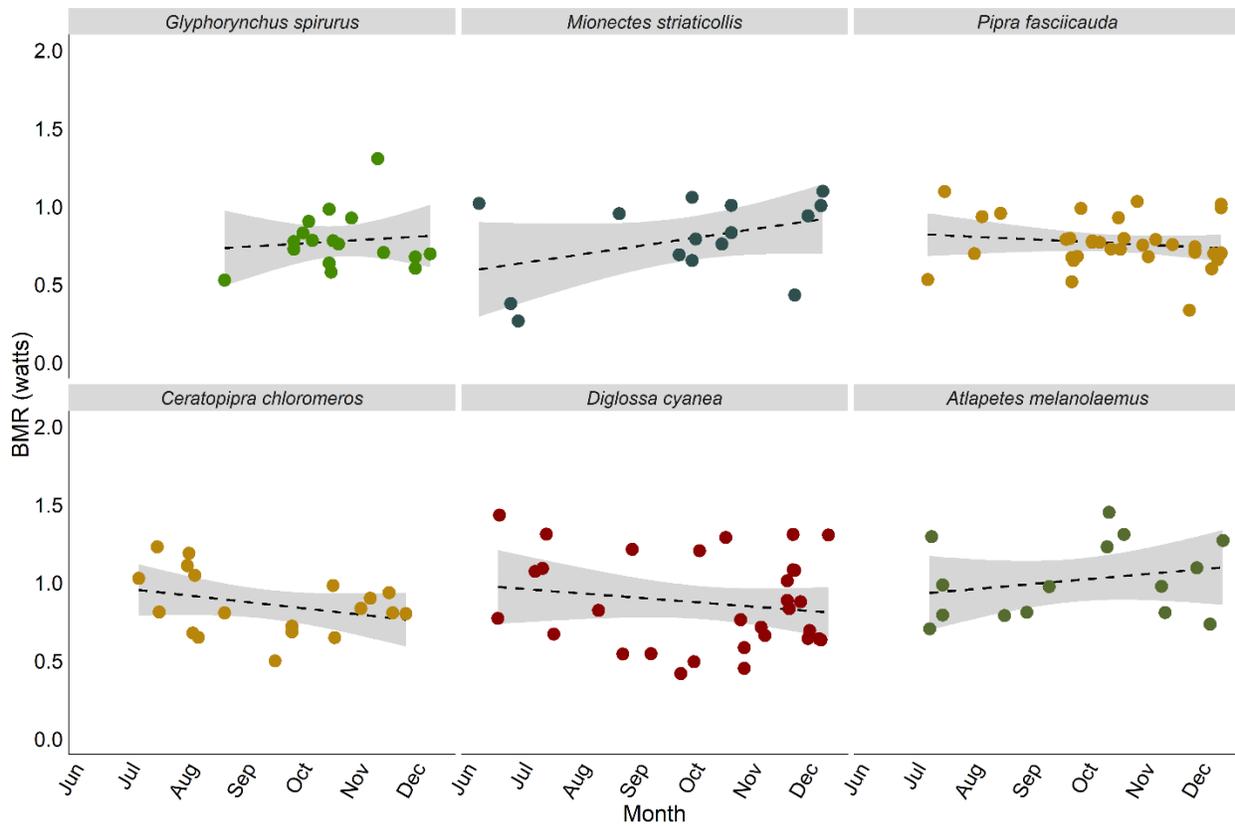


Figure B.2 Variation in basal metabolic rate (BMR) of tropical birds by season where June–July = dry season, August–September = transitional season, and October–November = wet season.

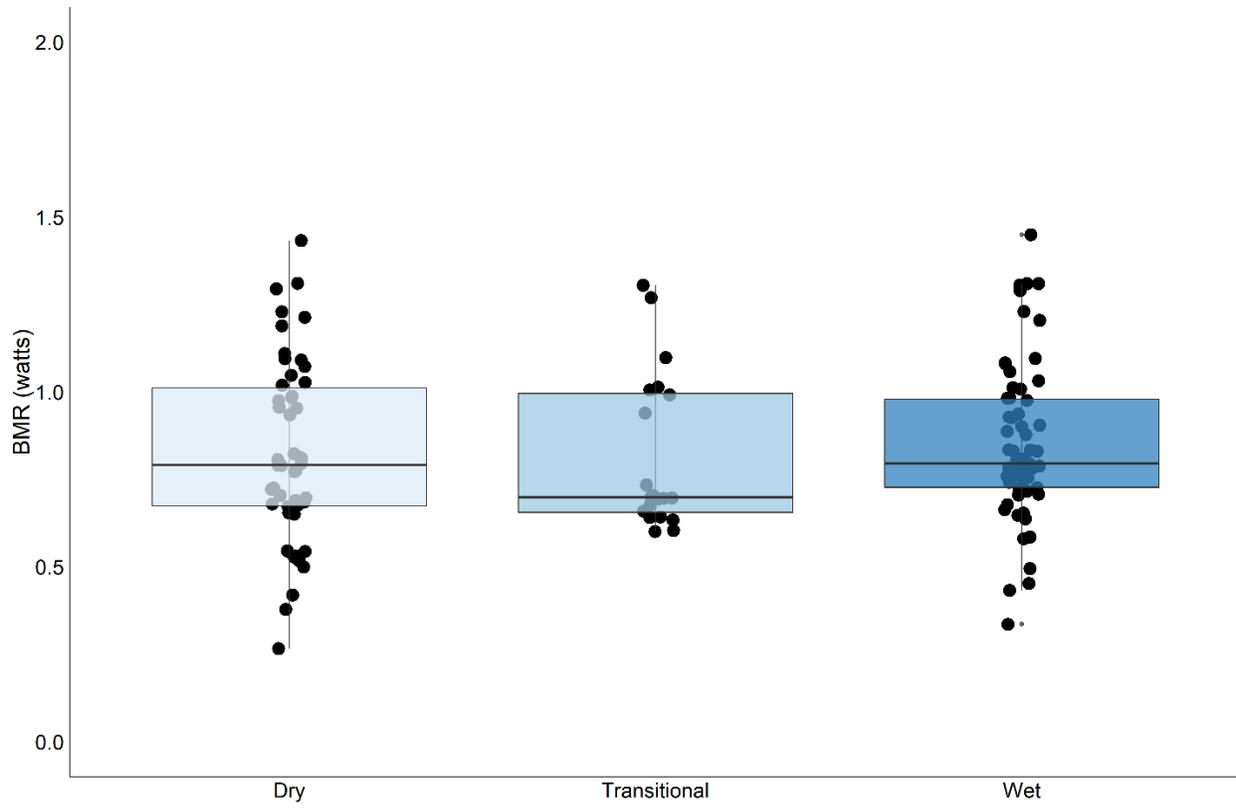


Figure B.3 Phylogenetic relationships of the 37 species of Neotropical passerines used in this study.

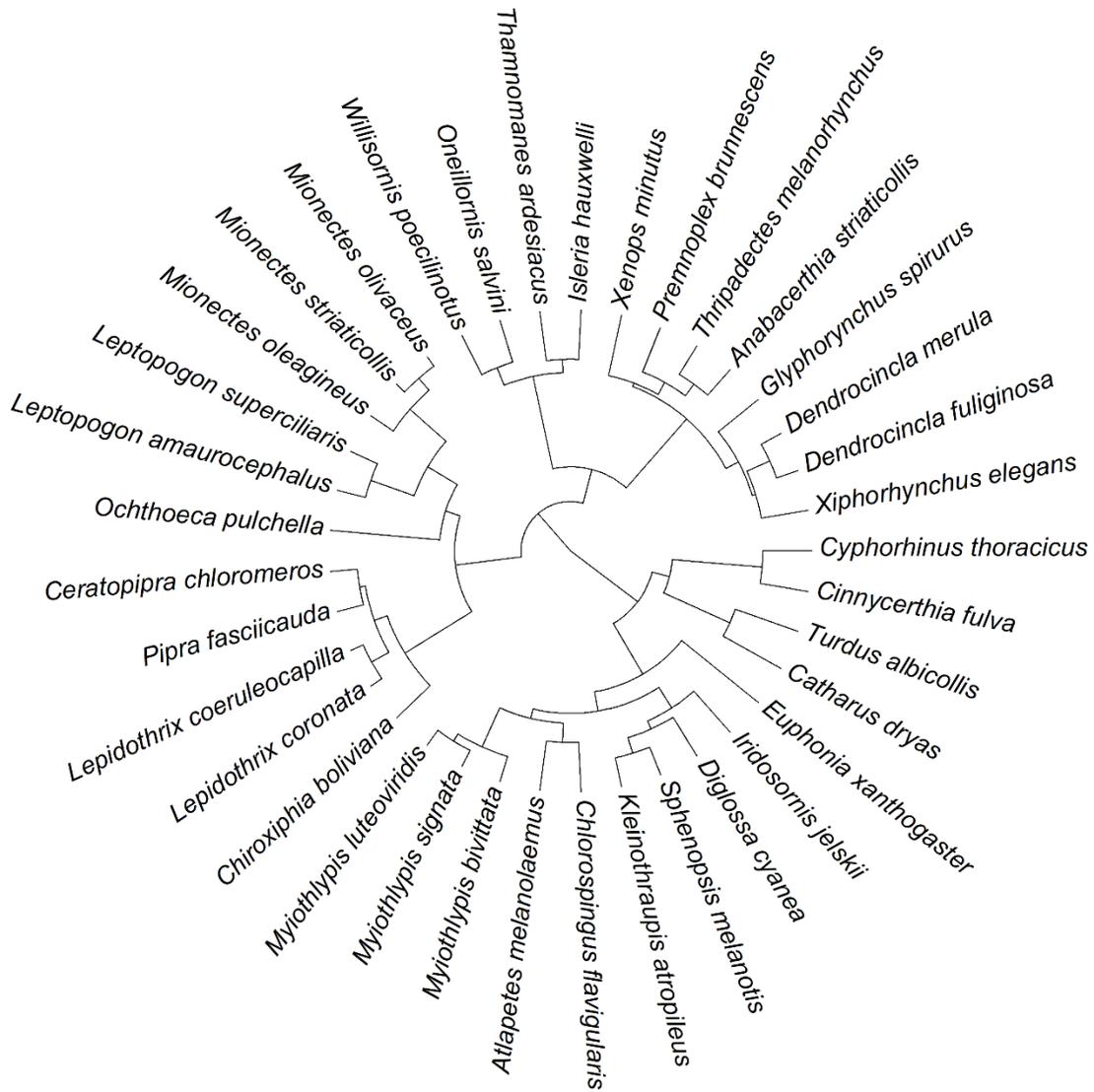
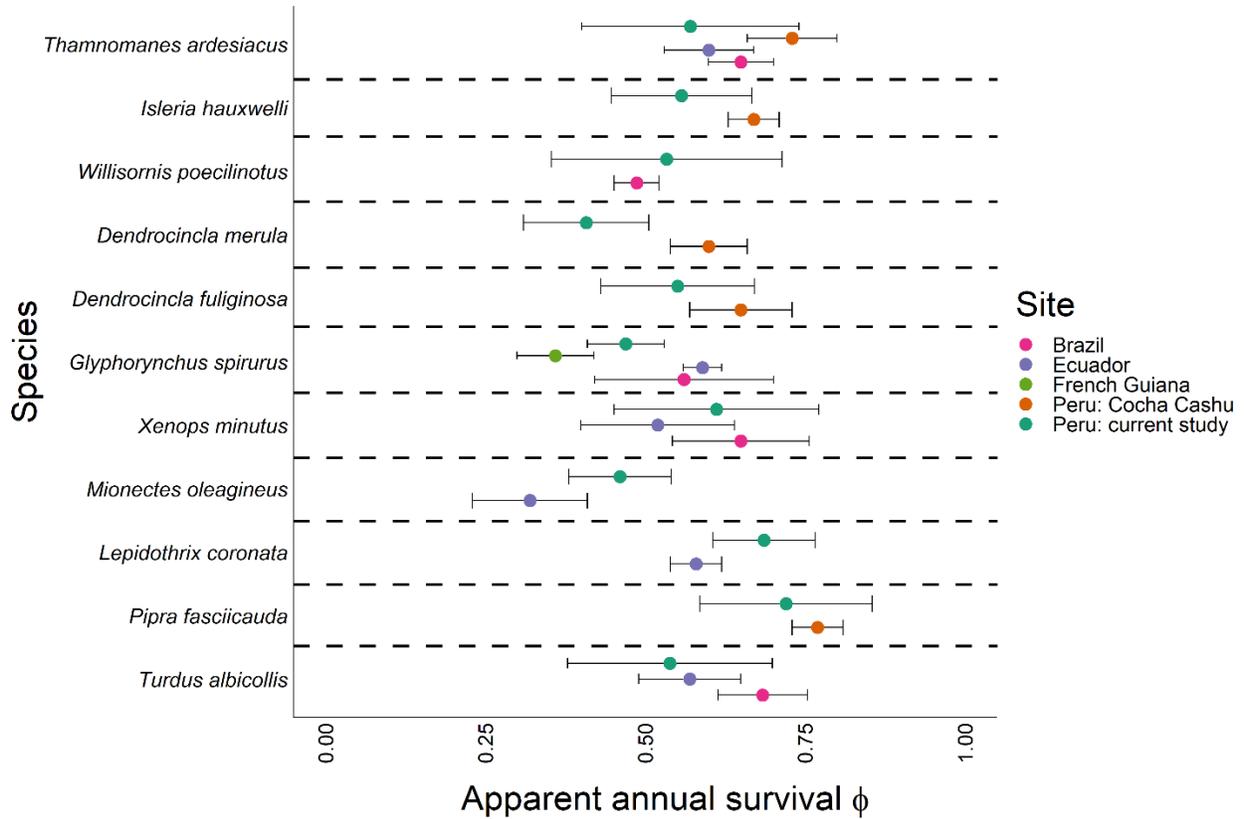


Figure B.4 Survival estimates and their associated standard errors compared across 11 species that co-occur throughout Amazonia. Brazil data are from Wolfe, Stouffer, & Seeholzer (2014); Ecuador data from Blake & Loiselle (2008); French Guiana data from Jullien & Clobert (2000); Cocha Cashu, Peru data from Francis, Terborgh, & Fitzpatrick (1999); other Peru data from this study.



Appendix C: Chapter 4 supplemental information

Chapter 4 Supplementary tables Studies of molt in South America

Table C.1 Sources providing information on the preformative molt in South American birds

Source of molt data	No. of species reported	Country of study
(Mallet-Rodrigues et al. 1995)	1	Brazil
(Castro-Astor et al. 2004)	1	Brazil
(Ryder and Durães 2005)	3	Ecuador
(Maia and Macedo 2011)	1	Brazil
(Botero-Delgadillo et al. 2012)	1	Brazil
(Gómez et al. 2012)	80	Colombia
(Hernández 2012)	5	Colombia
(Mallet-Rodrigues and Dutra 2012)	1	Brazil
(Ursino et al. 2012)	2	Argentina
(Araujo-quintero et al. 2015)	1	Venezuela
(Capllonch 2015)	3	Argentina
(Pyle et al. 2015)	26	Chile
(Del-Rio and Silveira 2016)	1	Brazil
(Moreno-palacios et al. 2017)	2	Colombia
(Norambuena et al. 2017)	1	Argentina and Chile
(Ortiz et al. 2017)	1	Argentina
(Chumpitaz-Trujillo et al. 2018)	1	Peru
(Cueva 2018)	1	Colombia
(Díaz and Hernández 2018)	1	Peru
(Díaz et al. 2018)	1	Peru
(Johnson and Wolfe 2018)	119	Brazil
(Kennedy et al. 2018)	10	Peru
(Llerena-Quiroz 2018)	1	Peru
(Antezana-Aponte 2019)	1	Peru
(Capllonch 2019)	1	Argentina
(Chumpitaz-Trujillo 2019)	1	Peru
(Scholer & Jankowski unpub. data)	64	Peru

Table C.2 List of manakin species with information on molt and plumage.

Species name	Common name	Source of molt and plumage data
<i>Pipra filicauda</i> *	Wire-tailed Manakin	Ryder & Durães 2005; Ryder & Sillett 2016
<i>Pipra fasciicauda</i>	Band-tailed Manakin	This study
<i>Dixiphia pipra</i>	White-crowned Manakin	Ryder & Durães 2005; Johnson & Wolfe 2018
<i>Ceratopipra erythrocephala</i>	Golden-headed Manakin	Johnson & Wolfe 2018
<i>Ceratopipra rubrocapilla</i>	Red-headed Manakin	Castro-Astor <i>et al.</i> 2004
<i>Ceratopipra chloromeros</i>	Round-tailed Manakin	This study
<i>Lepidothrix coronata</i>	Blue-crowned Manakin	Ryder & Durães 2005; This study
<i>Lepidothrix serena</i>	White-fronted Manakin	Johnson & Wolfe 2018
<i>Lepidothrix coeruleocapilla</i>	Cerulean-capped Manakin	This study
<i>Corapipo gutturalis</i>	White-throated Manakin	Johnson & Wolfe 2018
<i>Chiroxiphia linearis</i> *	Long-tailed Manakin	Foster 1987, McDonald 1993a, Doucet <i>et al.</i> 2007
<i>Chiroxiphia lanceolata</i> *	Lance-tailed Manakin	DuVal 2005, Araujo-quintero <i>et al.</i> 2015
<i>Chiroxiphia boliviana</i>	Yungas Manakin	This study
<i>Chiroxiphia caudata</i> *	Swallow-tailed Manakin	Foster 1987, Mallet-Rodrigues and Dutra 2012
<i>Manacus manacus</i>	White-bearded Manakin	Johnson & Wolfe 2018
<i>Machaeropterus pyrocephalus</i>	Fiery-capped Manakin	This study
<i>Cryptopipo holochlora</i>	Green Manakin	This study
<i>Neopelma chrysocephalum</i>	Saffron-crested Tyrant-Manakin	Johnson & Wolfe 2018
<i>Tyrannneutes virescens</i>	Tiny Tyrant-Manakin	Johnson & Wolfe 2018
<i>Piprites chloris</i>	Wing-barred Piprites	Johnson & Wolfe 2018

* Denotes species studied in a region other than South America.