

**SEASONALITY AND TRADE-OFFS IN EQUATORIAL
RUFIOUS-COLLARED SPARROWS
(*ZONOTRICHIA CAPENSIS*)**

Alexandra M. Class

Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State
University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Biological Sciences

Ignacio T. Moore,
Jeffrey R. Walters,
Marcella J. Kelley,
James D. Fraser,

11 November 2009
Blacksburg, Virginia

Keywords: seasonality, reproduction, territorial aggression, tropical, *Zonotrichia capensis*

Copyright © Alexandra M. Class 2009
This work may be copied provided credit is given and copies are not intended for sale

**SEASONALITY AND TRADE-OFFS IN EQUATORIAL
RUFIOUS-COLLARED SPARROWS (*ZONOTRICHIA CAPENSIS*)**

Alexandra M. Class

ABSTRACT

The majority of vertebrates are tropical, existing in an environment with low temperature seasonality. However, there is a strong research bias towards temperate-zone studies of seasonality. I investigated the timing of life history stages and trade-offs in tropical rufous-collared sparrows (*Zonotrichia capensis*) in the humid Andes of Ecuador, then compared my data to temperate-zone *Zonotrichia*. In Chapter II, I investigated the function of male territorial aggression. Males had peak territorial aggression scores during pre-breeding and nesting, suggesting that paternity protection and food resource defense are the primary selective forces shaping male territorial behavior. Territorial aggression responses depended on the life history stage of males, which were not synchronized within the general population. In Chapter III, I tested for a trade-off between male territorial aggression scores and paternal provisioning rate. Males with higher provisioning rates had nestlings with larger body size, but contrary to the findings of previous studies, there was no direct relationship between aggression and paternal provisioning. In Chapter IV, I investigated how *Z. capensis* allocated supplemental food. Previous studies (mainly in temperate-zone breeding birds) found food supplements were allocated to reproduction. We supplemented fed birds in both non-breeding and feeding fledglings life history stages; both groups molted (replaced feathers) in response to supplementation, thus invested in their own maintenance over immediate reproduction. In Chapter V, I tested whether latitude and/or altitude are good predictors of reproductive synchrony in *Zonotrichia*. Reproductive synchrony indices overlapped among tropical and temperate populations. The high altitude, temperate-zone *Zonotrichia* population had the highest synchrony index, but there was only a weak relationship of altitude in a comparison of tropical populations. Cumulatively I found that tropical humid-forest resident *Z. capensis* time life history stages according to individual condition and history and not by overarching climatic cues.

DEDICATION

To the animals, plants, nightscapes and thunderstorms that blanketed the Ecuadorian Andes. I will never forget your magnificence.

ACKNOWLEDGEMENTS

To all of the members of my committee, Dr. Ignacio Moore, Dr. Jeff Walters, Dr. Marcella Kelly, Dr James Fraser, I thank you for your time and effort, advice on experimental design, critique of my writing and in encouraging my research. Particularly to my advisor, Dr. Ignacio Moore, thank you for your time and help in finishing this dissertation in a timely manner.

I would also like to acknowledge the countless scientists and explorers that inspired me from early childhood. To Dr. F. Joyce and Dr. J. Chaves, my early tropical ornithology roots grew stronger from your guidance. To Dr. Anjali Kumar – our shared regard for adventure kindled my spirit and drive for tropical ecology outside of academia. To Bill Phillips and Fernando Game your support of my field work was essential, thank you. To Ursula Campos, your insight, love and energy helped me through many hard times. To Los Flacos and Enmita Palacios – long rides, patching tires, washing cow-manuer-soaked clothes, making empanadas at midnight and watching rainbows cloak the Andes at dusk made my experience precious. La familia de Rafa y Rafa your warm home, especially when I was very ill, helped me get through rough field seasons. To Dr. Haruka Wada, we met in the mountains, then again at the sea, then flowed each other to mountains on the other side. You are a continual inspiration. To all the advisors and friends that have encouraged me to learn, grow and challenge myself, especially Dr. Tom Hahn, Dr. Steve Schoech, Dr. Jeff Walters and Dr. Bill Hopkins.

To my family who have always supported my adventures. To my mom, Mary Class, who always told me to chase after my bliss. To the Freeman family, who have become close to my heart and taken me into their wilds – I look forward to a future of stunning biology and art experiences with you all.

To Benjamin Freeman, I do not think I would not have made it through without you. Thank you for you being where you were when you were, for your tireless love, sharp mind, and wild, unchallenged spirit.

TABLE OF CONTENTS

| | |
|-----------------------------------------------------------------------------------------------------------------------|-------------|
| ABSTRACT | ii |
| DEDICATION | iii |
| ACKNOWLEDGEMENTS | iv |
| TABLE OF CONTENTS | v |
| LIST OF FIGURES | viii |
| LIST OF TABLES | ix |
| ATTRIBUTION | x |
| | |
| CHAPTER I. SEASONALITY ACROSS LATITUDES | 1 |
| Introduction | 1 |
| Background | 1 |
| <i>Seasonality</i> | 1 |
| <i>The timing of life cycles in seasonal environments: endogenous rhythms & regulatory cues</i> | 2 |
| <i>A different strategy: opportunism</i> | 5 |
| <i>Seasonality in the tropics</i> | 5 |
| Zonotrichia: a unique system for comparative biology | 6 |
| <i>The genus Zonotrichia</i> | 6 |
| <i>Colombian Zonotrichia capensis</i> | 8 |
| <i>Costa Rican and Panamanian Zonotrichia capensis</i> | 10 |
| <i>Peruvian Zonotrichia capensis</i> | 11 |
| <i>Ecuadorian Zonotrichia capensis</i> | 11 |
| Study rationale and focus | 12 |
| <i>Chapter II. Male territorial responsiveness in different life history stages</i> | 13 |
| <i>Chapter III. Paternal care versus aggression</i> | 13 |
| <i>Chapter IV. Tropical slow pace of life and response to food supplementation</i> ... | 14 |
| <i>Chapter V. Reproductive synchrony and seasonality of life history stages</i> | 14 |
| Conclusions | 14 |
| Literature Cited | 15 |
| | |
| CHAPTER II. TERRITORIAL AGGRESSION IN TROPICAL RESIDENT RUFIOUS-COLLARED SPARROWS (ZONOTRICHIA CAPENSIS) | 25 |
| Abstract | 25 |
| Introduction | 26 |
| Methods | 30 |
| <i>Study population and life history stages</i> | 30 |
| <i>Definition of territories and simulated territorial intrusion protocol</i> | 31 |
| <i>Data analyses</i> | 32 |
| Results | 33 |
| <i>Aggression responses across life history stages</i> | 33 |
| <i>Comparisons of individual behavioral responses</i> | 34 |
| <i>Synchrony of life history stages</i> | 34 |
| Discussion | 35 |
| <i>Evaluating selective forces on territorial aggression</i> | 35 |

| | |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| <i>The timing of life history stages and population-level synchrony</i> | 37 |
| <i>Conclusions</i> | 39 |
| Acknowledgements | 40 |
| Literature Cited | 40 |
| | |
| CHAPTER III. IS THERE A TRADE-OFF BETWEEN CARING FOR OFFSPRING AND TERRITORIAL AGGRESSION IN TROPICAL MALE RUFIOUS-COLLARED SPARROWS (<i>ZONOTRICHIA CAPENSIS</i>)? | 53 |
| Abstract | 53 |
| Introduction | 54 |
| Methods | 57 |
| <i>Focal site, population and monitoring</i> | 57 |
| <i>Defining territories and nestling age classes</i> | 58 |
| <i>Provisioning observations</i> | 59 |
| <i>Simulated territorial intrusion protocol</i> | 59 |
| <i>Data analysis</i> | 60 |
| Results | 61 |
| <i>Effect of treatment and age class</i> | 61 |
| <i>Vigilance and provisioning rate versus aggression scores</i> | 61 |
| <i>Female versus male provisioning rate</i> | 62 |
| <i>Nestling body size index and provisioning rate</i> | 62 |
| Discussion | 62 |
| Acknowledgments | 65 |
| Literature Cited | 65 |
| | |
| CHAPTER IV. FOOD SUPPLEMENTATION PROMOTES MOLT IN A TROPICAL BIRD | 80 |
| Abstract | 80 |
| Introduction | 81 |
| Methods | 83 |
| <i>Study site and species</i> | 83 |
| <i>Assigning life history stages</i> | 83 |
| <i>Experimental design</i> | 84 |
| <i>Feeder stations and food supplements</i> | 84 |
| <i>Data analysis</i> | 85 |
| Results | 86 |
| Discussion | 87 |
| Acknowledgements | 91 |
| Literature Cited | 91 |
| | |
| CHAPTER V. THE TIMING OF LIFE HISTORY STAGES ACROSS LATITUDES IN <i>ZONOTRICHIA</i> SPARROWS | 99 |
| Abstract | 99 |
| Introduction | 100 |
| Methods | 103 |
| <i>Temperate Zonotrichia and study sites</i> | 103 |
| <i>Tropical Zonotrichia and study sites</i> | 104 |

| | |
|--------------------------------------------------------------------------------------------------------|-----|
| <i>Studying life history stages in Las Caucheras</i> | 105 |
| <i>Designating life history stages in Las Caucheras</i> | 106 |
| <i>Calculation of synchrony indices</i> | 107 |
| Results | 108 |
| <i>Climate</i> | 108 |
| <i>Population-level seasonality in Las Caucheras</i> | 108 |
| <i>Individual-level seasonality in Las Caucheras</i> | 109 |
| <i>Reproductive synchrony indices</i> | 109 |
| Discussion | 109 |
| <i>Comparing seasonality using reproductive synchrony indices</i> | 109 |
| <i>Factors affecting reproductive synchrony</i> | 110 |
| <i>Seasonality of life history stages in a mid-altitude equatorial population, Las Caucheras</i> | 111 |
| <i>Conclusions</i> | 112 |
| Acknowledgements | 113 |
| Literature Cited | 114 |

CHAPTER VI. LOW AMPLITUDE SEASONALITY AND TRADE-OFFS BETWEEN MOLT AND BREEDING LIFE HISTORY STAGES IN EQUATORIAL RUFOUS-COLLARED SPARROWS,

| | |
|--------------------------------------------------------------------------------|------------|
| ZONOTRICHIA CAPENSIS | 125 |
| Las Caucheras population-level seasonality | 125 |
| Cue response systems and timing life cycles to the environment | 125 |
| Factors influencing aseasonality in bird populations | 126 |
| <i>Timing life cycles to less than a year</i> | 128 |
| Mechanisms for timing life history stages in <i>Z. capensis</i> | 130 |
| Molt and fitness trade-offs in the timing of life history stages | 132 |
| <i>Molt in food supplemented pairs of <i>Z. capensis</i></i> | 135 |
| Constraints on timing life history stages within monogamous pairs | 136 |
| Future directions | 137 |
| Conclusions | 137 |
| Literature Cited | 138 |

LIST OF FIGURES

| | |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Figure 1.1 Satellite map of the Las Caucheras study site in Ecuador, South America... | 24 |
| Figure 2.1 Mean aggression scores (\pm SE) among males in five life history stages..... | 50 |
| Figure 2.2 The proportion of territories in each life history stage during two periods (March - June and September - December 2007)..... | 52 |
| Figure 3.1 Relationship between vigilance and aggression scores of breeding territorial males..... | 75 |
| Figure 3.2 Relationship between female and male provisioning..... | 76 |
| Figure 3.3 Relationship between nestling body size index and provisioning rates..... | 78 |
| Figure 4.1 Mean mass (g) \pm SE pre- and post-treatment for focal individuals..... | 96 |
| Figure 4.2 The proportion of individuals recaptured post-treatment in each life history stage in the non-breeding experiment and feeding fledglings experiment..... | 98 |
| Figure 5.1 Climate data from the four field sites..... | 122 |
| Figure 5.2 Life history stages of <i>Z. capensis</i> captured throughout the calendar year.... | 124 |

LIST OF TABLES

| | |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Table 2.1 Characteristics and observations used to determine five life history stages of individuals..... | 46 |
| Table 2.2 Principal component 1 (PC1) loadings for behavioral responses to simulated territorial intrusions in five different life history stages..... | 47 |
| Table 2.3 Aggressive behaviors divided among simulated territorial intrusion periods (pre-STI, STI, post-STI) and among life history stages..... | 48 |
| Table 3.1 Developmental characteristics by age class of nestling <i>Zonotrichia capensis</i> | 72 |
| Table 3.2 Principal component 1 (PC1) loadings for behavioral responses to simulated territorial intrusions in three nestling age classes..... | 73 |
| Table 3.3 Provisioning rates vs. vigilance and aggression scores..... | 74 |
| Table 4.1 Definition of life history stages..... | 95 |
| Table 5.1 Individual recaptured <i>Zonotrichia capensis</i> | 119 |
| Table 5.2 Synchrony indices for four <i>Zonotrichia</i> populations..... | 121 |

ATTRIBUTION

Dr. Ignacio T. Moore

Associate Professor, Department of Biological Sciences, 2119 Derring Hall, Virginia
Polytechnic Institute and State University, Blacksburg, Virginia 24061

Dr. Ignacio T. Moore was my advisor throughout my dissertation research and chaired my dissertation committee. He also was the co-author of manuscripts in preparation for publication, including all of the data chapters of my dissertation.

CHAPTER I. SEASONALITY ACROSS LATITUDES

Introduction

The tropics (between the Tropic of Cancer and the Tropic of Capricorn 23°26'N, S, respectively) is the most species-rich and diverse region on earth (Wilson 1999). However, comparatively little research has focused on the behavioral ecology of animals in tropical latitudes (Wilson 1999; Stutchbury & Morton 2001). Among bird species, the vast majority (e.g., ~80% of passerines) breed in the tropics, but most are poorly known (Martin 1996; Stutchbury & Morton 2001, 2008). Of tropical birds that have been studied, there is considerable diversity in life history characteristics, territorial systems and behavior (Stutchbury & Morton 2001, 2008). However, there is a considerable temperate-zone research bias which hinders broad comparisons of temperate-zone and tropical birds. My dissertation investigates the timing of life history stages, behavior and life history trade-offs in a tropical bird species, the rufous-collared sparrow (*Zonotrichia capensis*) and compares the life history of this tropical resident species with temperate-zone congeners.

Background

Seasonality

Animals time life history stages (e.g., reproduction, migration) according to the seasonality of the environment(s) in which they exist (Jacobs & Wingfield 2000; Stutchbury & Morton 2001; Wingfield 2008). Highly seasonal environments are characterized by distinct annual climatic cycles, which predict seasonal fluctuation in resources (Lofts & Murton 1968; Murton & Westwood 1977). Animals can therefore use predictable seasonal environmental change to schedule energetically expensive behaviors, like reproduction, in advance of seasonal periods when resources will be most abundant and available (e.g., spring and summer seasons) (Lofts & Murton 1968; Murton & Westwood 1977; Dawson et al. 2001). To take full advantage of seasonal cycles in the environment, organisms have evolved precise and rapid responsiveness to cues that signal characteristic seasonal changes (Marshall 1970; Cockrem 1995; Dawson et al. 2001; Brown et al. 2002; Dawson 2008; Hahn & MacDougall-Shackleton 2008; Wikelski et al. 2008).

The timing of life cycles in seasonal environments: endogenous rhythms and regulatory cues

Endogenous rhythms (internal timing mechanisms) provide a basic temporal framework into which environment-specific external regulatory cues may be integrated. Endogenous rhythms therefore can buffer organisms against misleading information that might otherwise lead to the mistimed initiation of a life history stage (e.g., a warm week in the middle of winter will not lead to breeding initiation) (Murton & Westwood 1977; Gwinner 1986). Environmental regulatory cues used to adjust endogenous rhythms to be in tune with the external environment are classified into four categories: 1) initial predictive: long-term cues that can predict future environmental change, such as photoperiod (day length), 2) supplementary: short-term environmental cues that typically act as secondary mechanisms to fine-tune initial predictive cues, such as food availability, 3) synchronizing: short-term cues that promote synchronization of a pair or group, such as social interactions and 4) modifying: short-term cues that disrupt or delay a life cycle stage, such as late-spring snow storms (Farner & Wingfield 1978; Wingfield & Farner 1980; Dawson 2001). Thus, organisms are thought to rely on endogenous rhythms as a template for predictions about the long-term schedule of environmental conditions, whereas other cues are used to fine-tune and describe short-term changes in environmental or social conditions (Hamner & Stocking 1970; Farner & Wingfield 1978; Hahn et al. 1992; Lambrechts et al. 1996; Hau et al. 2000; Wikelski et al. 2008; Helm et al. 2009).

Research on the seasonality of animal behavior has historically focused on species breeding in the temperate-zone, an environment with characteristic annual seasonal cycles (Lofts & Murton 1968; Murton & Westwood 1977; Wingfield et al. 1992; Ball 1993; Cockrem 1995). It is well-established that in mid- to high latitudes photoperiod is the most universal initial predictive cue used to time life history stages (Lofts & Murton 1968; Perrins 1970; Murton & Westwood 1977; Daan et al. 1986; Dawson et al. 2001). Changes in photoperiod stimulate physiological change, often via neuroendocrine pathways (for review see Lofts and Murton 1968; Murton and Westwood 1977; Dawson et al. 2001). Thus, in seasonal environments where photoperiod changes are detectable, seasonal physiological changes in response to photoperiodic cues are primarily responsible for the timing of life history stages (Lofts & Murton 1968; Murton & Westwood 1977; Daan et al. 1986; Ball 1993; Dawson et al. 2001; Helm et al. 2009).

To fine-tune physiological and behavioral processes, animals rely on supplementary and synchronizing cues that often correlate with changes in initial predictive cues (Hamner &

Stocking 1970; Hahn et al. 1992; Lambrechts et al. 1996; Hau et al. 2000; Helm et al. 2006). For instance, many bird species breeding in the temperate-zone can use seasonal increases in daily temperature to fine-tune predictions of increasing insect abundance in early spring (Lack 1954; Perrins 1970; Hahn et al. 1992; Wingfield et al. 1992; Wingfield et al. 1996). Rainfall is an important supplementary cue for many species existing in drier habitats with seasonal monsoons (Illera & Díaz 2006; Strand et al. 2007). Food availability in itself is a particularly important supplementary cue in that it is a direct (via nutrient and energy supply) and indirect (via visual and tactile stimuli) stimulus for reproductive physiology and behavior (Lack 1954, 1968; Wingfield & Farner 1980; Schoech 1996; Schoech & Hahn 2005; Schoech & Hahn 2008). Further, there is a tight correlation between peaks in food abundance and successful breeding attempts in most species examined to date (Daan et al. 1986; Schoech 1996; Aparicio & Bonal 2002; Schoech et al. 2004; Schoech & Hahn 2008). Additional fine-tuning of seasonal timing may come from social cues that synchronize reproductive efforts within populations or between pairs of birds (Moore 1983; Wingfield 2005; Helm et al. 2006). A combination of supplementary and synchronizing cues may permit finer-scale tuning of the timing of life history stages with the local environment (Hau 2001; Stutchbury and Morton 2001).

The ability of animals to make use of fluctuations in the environment to time life history stages depends on the predictability of seasonal fluctuations (do they occur at the same time each year?) and the amplitude of seasonal fluctuations (are changes detectible?) (Colwell 1974; Wingfield et al. 1992; Wingfield et al. 2000; Dawson 2008). Typically, interannual predictability of seasonal environmental fluctuations and the amplitude of seasonal fluctuations decline with latitude (Colwell 1974; Wingfield et al. 1992). There is also less seasonal change in photoperiod at lower latitudes. Therefore, in tropical regions photoperiod may not be the most meaningful cue for long-term predictions about the seasonal climate (Colwell 1974; Wingfield & Farner 1980; Hau 2001; Scheuerlein & Gwinner 2002; Dawson 2008; Small & Moore 2009). Instead, multiple cues, or cues other than photoperiod – such as food availability or rainfall (cues often considered to be supplementary in the temperate-zone) – can be used to time life history stages (Colwell 1974; Komdeur 1996; Hau 2001; Scheuerlein & Gwinner 2002; Hau et al. 2004; Komdeur & Daan 2005; Hau 2008; Perfito et al. 2008).

Most species use endogenous rhythms in concert with regulatory cues to time life history stages. Endogenous rhythms continuously cycle during the lifetime of an organism and are

thought to be inherited (Farner & Gwinner 1980; Dittami & Gwinner 1985; Helm et al. 2009). Each organism has a distinct endogenous rhythm maintained through time that inherently deviates from a 24 hours per day/ 365 days per year cycle (Gwinner 1996; Dittami & Gwinner 1985; Wikelski et al. 2008). Thus organisms can reset their internal clock to be in tune with habitat-specific “zeitgebers”, or environmental cues that are used to synchronize endogenous rhythms with the environment, so that life history stages are optimized to current environmental conditions (Gwinner 1996; Paul et al. 2008; Wikelski et al. 2008).

In an exemplary study of endogenous rhythms, equatorial stonechats (*Saxicola torquata*) were removed from their environment before hatching and placed in laboratory chambers with unchanging conditions (Gwinner & Dittami 1990). Seasonal growth of the gonads occurred according to individual internal rhythms of gonadal development (Gwinner & Dittami 1990). Indeed, *S. torquata* subjects showed circannual endogenous rhythms in physiology and behavior that persisted over the duration of their lives (7 - 9 years; Gwinner & Dittami 1990). However, since synchronizing cues were absent, individual rhythms of gonadal development and recrudescence deviated from the 365 day year (Gwinner & Dittami 1990). Similarly, chaffinches (*Fringilla coelebs*) that were kept under constant dim light had daily activity cycles lasting slightly less than 24 hours (Aschoff 1980). However, chaffinches allowed to synchronize their endogenous clock to natural photoperiod remained on annual schedules appropriate for their external environment (Aschoff 1980).

Though the advantages of maintaining endogenous rhythms of behavior are still debated (Webster et al. 2002; Menaker 2006; Dawson 2007; Buehler & Piersma 2008; Wikelski et al. 2008), endogenous cycles are hypothesized to evolve under less seasonal environmental cycles, where precise timing of life history stages may not be as critical to fitness (Scheuerlein & Gwinner 2002). Unfortunately, hypotheses about the evolution and persistence of endogenous cues are inherently difficult to test (Wikelski et al. 2008). Experiments examining endogenous rhythms either: 1) require long-term laboratory experiments conducted via the complete removal of animals from their environment or 2) will be confounded in field experiments by the fact that endogenous rhythms are synchronized with specific environmental cues (Paul et al. 2008; Wikelski et al. 2008; Helm et al. 2009).

A different strategy: opportunism

In environments without predictable and/or strong seasonality, animals may be able to time energetically expensive life history stages to unpredictable periods with favorable resources (Hahn 1995; Emerson & Hess 1996; Deviche & Sharp 2001; Hau et al. 2004; Hahn & MacDougall-Shackleton 2008). For example, in crossbills (*genus Loxia*), zebra finches (*Taeniopygia guttata*) and Galápagos small ground finches (*Geospiza fuliginosa*), reproductive opportunism is influenced by the fact that their primary food resource is not seasonally predictable (Boag & Grant 1984; Hahn et al. 1995, 1998; Deviche & Sharp 2001; Chandola-Saklani et al. 2004; Hau et al. 2004; Hahn & MacDougall-Shackleton 2008). *Taeniopygia guttata* appear to rely on cues from erratic cycles in rainfall and humidity to predict relative abundance of their arid grass-seed prior to initiating breeding, but wait for grass seeding to fully commit to breeding (Perfito et al. 2006; Perfito et al. 2007). A similar situation occurs with *G. fuliginosa* on the Galápagos, which breed opportunistically in response to high rainfall or cues associated with high rainfall (Boag & Grant 1984; Hau et al. 2004). Crossbills of the *genus Loxia* take advantage of sporadically abundant green pinecone crops which loosely associate with intra-decadal climatic cycles in North America and do not use any single environmental cue to predict seed masting (Hahn 1995, 1998; Hahn et al. 1995; Hahn & MacDougall-Shackleton 2008). However, crossbills are not strict opportunists because they do not breed during an autumnal photorefractory phase (where reproductive stimulation is not possible in short photoperiod), even in response to favorable food cues (Hahn & MacDougall-Shackleton 2008). Opportunistic strategies evolve in response to environmental and resource unpredictability, and appear to be more common in species inhabiting arid environments (e.g., *T. guttata*, *G. fuliginosa*) or species with extremely specific and unpredictable food requirements (birds in the *genus Loxia*).

Seasonality in the tropics

Many tropical bird species breed seasonally (Stutchbury & Morton 2001, 2008) and three proposed mechanisms to time tropical seasonality have gained support. *The first mechanism* considers photoperiod to be an important initial predictive cue for tropical organisms. In Panama, spotted antbirds (*Hylophylax naevioides*) respond to as little as 17 min. annual shift in photoperiod, suggesting tropical birds can be sensitive to low-latitude photoperiodic cues (Hau et al. 1998; Beebe et al. 2005). However, spotted antbirds rely heavily on supplemental cues to time

reproductive behaviors, including visual and social cues related to food abundance (Hau et al. 1998). Thus, photoperiod may be an initial predictive cue for some low-latitude species. However, low amplitude temperature and rainfall seasonality in the tropics may make initial predictions via photoperiod less accurate, so reliance on other cues may be essential to tune predictions to the local environment.

A second mechanism proposed for seasonal reproductive regulation of tropical vertebrates involves endogenous rhythms. Unlike spotted antbirds, *S. torquata* and red-billed quelea (*Quelea quelea*) do not respond to the minimal annual changes in equatorial photoperiod as an initial predictive cue (Lofts 1964). Instead, *S. torquata* and *Q. quelea* have endogenous circannual rhythms that are synchronized to the local equatorial environment principally by cues related to rainfall (e.g., reproductive physiology and behavior is up-regulated at the transition from dry to rainy periods) (Lofts 1964; Dittami & Gwinner 1990; Wikelski et al. 2003). Thus, the annual reproductive cycle of *S. torquata* and *Q. quelea* on the equator is synchronized with the 365-day year (Lofts 1964).

A third mechanism proposed is that tropical animals are largely opportunistic. Since there may be a lack of reliable initial predictive cues in many low-latitude systems, fluctuations in resources may occur more sporadically (Hau et al. 2004; Perfito et al. 2007). Consequently, increased flexibility of the reproductive biology and behavior may result. *Taeniopygia guttata* show resource opportunism in that they can mate at any time of the year if resources and the climate become favorable (Perfito et al. 2007; 2008). In *G. fuliginosa*, of the Galápagos Islands, reproductive opportunism is coupled with seasonal gonadal regression (Hau et al. 2004). The regression of energetically costly reproductive structures most likely relates to energy conservation in periods that are less likely to have abundant resources available (Hau et al. 2004). However, unpredictable heavy rains cue the initiation of reproduction (Hau et al 2004). Thus some tropical passerines may be opportunists and take advantage of unpredictable fluctuations of resources at all times of the year.

***Zonotrichia*: a unique system for comparative biology**

The genus Zonotrichia

Five species of *Zonotrichia* breed from northern Alaska, *Z. leucophrys*, to Tierra del Fuego, Argentina, *Z. capensis*, and from sea-level to 5300 meters (Blanchard 1941; Bent 1968; Miller &

Miller 1968; Morton 2002). *Zonotrichia* populations also occupy diverse habitats including coastal chaparral or xeric communities, city parks, subalpine meadows and páramo grasslands (e.g., Chapman 1940; Blanchard 1941; Morton 2002; Bent 1968). Members of the genus *Zonotrichia* are among the best studied bird species in the world (e.g., Chapman 1940; Blanchard 1941; Zink & Blackwell 1996; Morton 2002; Moore et al. 2005). Thus, investigations of tropical *Zonotrichia* can add to our knowledge of tropical systems while remaining within a well-studied genus, eliminating phylogenetic confounds which often hinder broader comparisons among tropical and non-tropical species.

Across their range *Zonotrichia* have sexually monomorphic plumage, are socially monogamous, and generally exhibit biparental care (Blanchard 1941; King et al. 1966; Miller & Miller 1968; Wolf 1969; Kalma 1970; Davis 1971; Morton 2002). However, *Zonotrichia* exhibit a wide array of life history characteristics. Largely depending on breeding latitude, *Zonotrichia* can be migratory (austral, altitudinal, or intracontinental) or sedentary (Chapman 1940; Blanchard 1941; King et al. 1966; Morton 2002). Clutch sizes generally increase with latitude (e.g., a clutch of 2 is common among near-equatorial *Zonotrichia* (Miller & Miller 1968; Kalma 1970), but a clutch of four or more is common in North temperate-zone *Zonotrichia* (Morton 2002)).

As in the majority of temperate-breeding animals, temperate-breeding *Zonotrichia* use photoperiod cues as the primary predictive cue for seasonal timing of reproductive physiology and behavior (Wingfield & Farner 1980; Wingfield & Moore 1987). Experiments have demonstrated that near-equatorial *Z. capensis* can perceive typical temperate-zone photoperiod (Miller 1959b; Miller 1965). However the near-equatorial photoperiod varies minimally, thus near-equatorial residents 1) may not be able to perceive minimal daily change in photoperiod or 2) may not use photoperiod as the primary predictive cue for timing life history stages because it does not relate to any significant seasonal variation in climate or the environment (Miller 1965).

Zonotrichia capensis is the only tropically ranging species in the genus *Zonotrichia* and is phylogenetically basal to the other four *Zonotrichia* species (Zink & Blackwell 1996). Just as in other species of *Zonotrichia*, populations of *Z. capensis* exist in diverse habitats including coastal deserts, humid forest gaps, urban areas and páramo grasslands. The range of *Z. capensis* is from Chiapas, Mexico to the Tierra del Fuego, Argentina, and 0 to 5300 m altitude (Chapman 1940; Davis 1971). Over 20 subspecies of *Z. capensis* are recognized across their latitudinal

range (Chapman 1940). The different subspecies demonstrate considerable variability in life history characteristics: they can be migratory or sedentary, eat a variety of seeds, insects and occasionally fruit, and have different temporal schedules for the timing and duration of life history stages (Chapman 1940; Miller & Miller 1968; Kalma 1970; King 1973; Moore et al. 2005). *Zonotrichia capensis* breed seasonally in several populations throughout their range: Costa Rica (Wolf 1969), Panama (Kalma 1970), Colombia (Miller 1959a; Miller 1962), Ecuador (Moore et al. 2005), Peru (Davis 1971), Chile (Novoa et al. 1996) and Argentina (King 1973). However, seasonal timing of reproduction is variable among the populations.

Colombian Zonotrichia capensis

Alden H. Miller studied the natural history of Colombian *Z. capensis*. Miller hoped to initiate a scientific comparison of congeners across latitudes, starting with *Z. capensis* (Miller & Miller 1968). The subject of Miller's investigations was a single Colombian population of *Z. capensis*, inhabiting the Western Andes of Colombia near Cali (3°50'N, 76°70'W; 6500 m altitude; Miller & Miller 1968). Miller found that the Colombian *Z. capensis* reproduced on a roughly seasonal, but bimodal schedule (Miller 1962; Miller & Miller 1968). Miller (1959a, 1962) suggested that the breeding cycles were loosely correlated with the end of the wettest parts of the year. However, Miller (1959a, Miller & Miller 1968) also thought food resources could factor into breeding timing. Nevertheless, no experimental examination of these suggested cues has been conducted. Molting schedules appeared to follow either bimodal or unimodal seasonality in this population (Miller 1961). Despite the approximate six-month periodicity of breeding and molting, some individuals in the population were noted as being in breeding condition at all times of the year (Miller 1959a, 1962). Miller believed that endogenous cycles were driving population-level synchrony, therefore that individuals had inherently different reproductive cycles (Miller 1959a, 1962; Miller & Miller 1968). Further, potential *zeitgebers* such as rainfall or temperature did not appear to unanimously explain the dual annual reproductive cycles in the Colombian *Z. capensis* population (Miller 1959a, 1965; Miller & Miller 1968).

In breeding pairs of Colombian *Z. capensis*, nestling care was noted as primarily maternal (Miller and Miller 1968). Paternal aggressiveness and presence in the territory was evident, but fathers spent considerably less time near the nest than mothers (Miller & Miller 1968). Miller also observed that grass seeds were continually abundant, and heterospecific granivorous

competitors were rare, suggesting that there was little competition for food resources (Miller & Miller 1968). Nestlings and juveniles were primarily fed a variety of insects that could be found throughout the year (Miller and Miller 1968).

Molt cycles in *Z. capensis* typically occur outside of breeding periods in Colombia (Miller 1961). Miller (1961) noted two complete molt cycles in some individuals in the population, separated by about six months on average. Miller hypothesized that bimodal annual molt cycles were necessary to maintain functional plumage; the abrasive, perennial grass where the birds foraged and frequent, severe rains were thought to cause substantial plumage wear (Miller 1961). He also predicted that the seasonal decline in rainfall, slight increase in ambient temperature, increase in periods of direct sunlight and lack of morning dew could influence the onset of annual molt cycles (Miller 1961). Thus, dual annual molt cycles may, in some *Z. capensis* populations, be an influential process affecting reproductive seasonality (Miller 1961).

Miller suggested that tropical *Z. capensis* demonstrated endogenous rhythms of behavior (Miller 1959a, b; Miller 1965). Miller (1965) was interested in determining whether near-equatorial *Z. capensis* had a similar photo-refractory phase as temperate congeners. To test if *Z. capensis* could perceive short photoperiod, Miller conducted several experiments. In one study, Miller (1965) tested if wild-caught young *Z. capensis* kept for several years under ambient photoperiod in Berkeley, California (38°N), would modify their behavioral cycles in response to temperate-zone photoperiodic changes. *Zonotrichia capensis* that were raised in outdoor aviaries initiated and/or maintained breeding condition under long photoperiod (longer than typical of equatorial latitudes; Miller 1965). However, Miller found that while male *Z. capensis* tended to prolong their natural breeding period irrespective of photoperiod change, sometimes growing and or maintaining reproductive condition in temperate-zone winter photoperiods, female *Z. capensis* did not initiate or prolong breeding in periods with short photoperiod (Miller 1965). The reason for the difference between female and male response to short photoperiod is still unclear (Miller 1965), but suggests females may limit breeding timing where photoperiod is a cue used to time seasonal reproduction. Miller believed that Colombian *Z. capensis* do not experience photoperiods short enough to go into photorefractory phase and therefore adhere to endogenous timing rhythms without a major *zeitgeber* in Colombia, but that these timing mechanisms are overridden by temperate latitude photoperiodic cues (Miller 1965).

Costa Rican and Panamanian Zonotrichia capensis

Wolf (1969) and Kalma (1970) studied the reproductive ecology and annual cycles of *Z. capensis* in Central America. Wolf (1969) studied *Z. capensis* in the central mountains of Costa Rica near the city of Vara Blanca (10°10'N, 84°15'W; 1800 - 2200 m altitude), while Kalma (1970) focused his research in three sites located in the Bugaba district of the western portion of the Province of Chiriqui, Panama (8°50'N, 82°60'W; 1500-1900 m altitude). Both Kalma (1970) and Wolf (1969) suggested that there were major and minor breeding periods, but that reproduction and molt were site-dependent in Central America. Thus, while *Z. capensis* in some sites appeared to follow one major cycle of breeding and molt per year, others had annual cycles consisting of a partial and complete molt and bimodal reproduction (Wolf 1969; Kalma 1970). In Costa Rican populations of *Z. capensis*, Wolf (1969) believed photoperiodic cues should be ruled out as predictive cues used to time reproduction because of the lack of tight breeding and molt schedules. However, Wolf's (1969) assumptions were made in a time when there were no experimental data showing photoperiodic sensitivity of resident tropical species at low latitudes and we now know photoperiod can be perceived and used as a predictive cue by another resident tropical bird species at Costa Rican latitudes (Hau et al. 1998).

In Panama and Costa Rica, differences in the abundance of food (primarily insects) may also be an important cue driving reproductive and/ or molt periodicity, as they are the major component of the diet of young *Z. capensis* (Kalma 1970; Miller 1961; Miller & Miller 1968). Panamanian populations *Z. capensis* bred at different times of the year, but primarily just prior to the onset of heavy rains, which predicted increased insect abundance according to Kalma (1970). Wolf (1969) had proposed that changes in the physical character of the land affecting the flora diversity could explain reproductive cycles in Costa Rican *Z. capensis*, as an alternative to photoperiodic changes, because he believed photoperiod changes at such low latitude could not be perceived. Kalma (1970) agreed with Wolf (1969) that landscape changes in resource availability (including food abundance due to rainfall seasonality) were potentially responsible for the timing of reproduction in Central American populations and that photoperiodic change was too minimal to be perceived, but also suggested genetic difference may play a role in different populations' timing of life history stages. However, Kalma's measures of prey abundance were inadequate to determine if fluctuations of insect abundance determined cycles in breeding and/or molting (Kalma 1970). Neither Kalma (1970) nor Wolf (1969) investigated

photoperiod detection in the wild and no research has readdressed these hypotheses in *Z. capensis* since the studies were published.

Peruvian Zonotrichia capensis

Davis (1971) studied the annual molt and reproduction schedules of *Z. capensis* in coastal desert near Chilca, outside of Lima, Peru (12° 30'S, 76°80'W; 25 m altitude). The main population inhabited an area dominated by irrigated citrus and cornfields. Davis (1971) found that the population of *Z. capensis* inhabiting the arid coast of Peru was almost entirely reliant on agricultural water due to the lack of regular rainfall and natural terrestrial water sources. However, *Z. capensis* were nearly all in breeding condition from October to December and nearly all molting from May through June (Davis 1971). Similar to the findings of Miller in Colombia, *Z. capensis* in Peru showed incomplete gonadal regression after breeding (Miller & Miller 1968; Davis 1971). Unlike *Z. capensis* studied in Colombia (Miller 1961), but similar to those studied in some populations in Costa Rica (Wolf 1969; Kalma 1970), *Z. capensis* in Peru had one partial molt prior to breeding and one complete molt after breeding (Davis 1971). In Peru male birds showed a strong and almost immediate recrudescence of gonads after molting was complete (Davis 1971). Just as in other populations of *Z. capensis*, insects represented a minor part of the diet compared to seeds (Davis 1971). However, fluctuating insect abundance seemed to predict the onset breeding in the *Z. capensis* studied in coastal Peru (Davis 1971). Though Davis (1971), as well as Kalma (1970) and Wolf (1969), agreed that photoperiod could not have been used as a predictive cue in their relatively low latitude study locations, more recent data from experiments on Panamanian *H. naevioides* suggests photoperiod could be perceived at Peruvian latitudes (Hau et al. 1998; Wikelski et al. 2000).

Ecuadorian Zonotrichia capensis

As in other populations of *Z. capensis*, some populations exhibit seasonality of life history stages on the equator (Moore et al. 2005). For instance, in Papallacta (0° 21'S, 78°09'W; 3300 m altitude), Ecuador, *Z. capensis* mainly breed during a 3-month breeding season from September to December (Moore et al. 2005). Molting schedules also appear to follow this unimodal seasonality (Moore pers. com.). In the population of Pintag (0° 22'S, 78°23' W; 2900 m altitude), Ecuador (only 25 km from Papallacta, but separated by the Andean divide), birds breed on

completely different annual schedules (Moore et al. 2005). Though no studies have explicitly tested what cues drive seasonality in equatorial *Z. capensis*, the birds appear to use a combination of environmental (e.g., rainfall) and social cues to synchronize breeding (Moore et al. 2005). It has also been hypothesized that breeding asynchrony between the Pintag and Papallacta populations may be the result of opposing annual rainfall schedules on the two sides of the Andean divide, possibly affecting annual food resource abundance (Moore et al. 2005). Since there is evidence that genetic differences exist between the two populations, asynchrony may be related to genetic adaptation to local cues (Moore et al. 2005). However much remains to be investigated in this system, especially in terms of how species in less seasonal equatorial populations (where photoperiod and major synchronizing cues may be imperceptible) organize life histories and what trade-offs exist that determine how time and energy are invested into specific activities.

Study rationale and focus

Most environments are to some extent seasonal. However, temperate-zone bias in research dominates our current understanding of the timing of life history stages within life cycles (Hau 2001; Stutchbury & Morton 2008). Tropical environments are characterized by less change in photoperiod and less seasonal fluctuation in temperature, with rainfall and food abundance potentially taking the place of other cues used for longer-term predictions of seasonal environmental cycles. In my dissertation I aimed to describe the timing of life history stages in a tropical population of birds in an environment characterized by low temperature and rainfall seasonality. I also wanted to learn how organisms existing in such environments behave, if they reproduce synchronously, and if they respond similarly to seasonal temperate-zone breeding species in terms of territorial aggression behavior and food resource manipulations.

I collected data from a focal population of *Z. capensis* located at mid-altitude (~2100 m) in the rural township of Las Caucheras in Napo province, Ecuador (0°37'S, 77°55'W; Figure 1.1). This population was selected because it is equatorial (there are minimal inputs from photoperiod) and seasonal climate is less pronounced than previously studied populations. Mean annual accumulated rainfall averages between 3150 - 3300 mm per year. Though there is consistent high rainfall and days without rainfall are rare, monthly accumulated rainfall is between 130 - 240 mm from October - March and 280 - 390 mm from April - September (Instituto Nacional de

Meteorológica, Ecuador). Mean monthly air temperature remains nearly constant throughout the year at $\sim 17^{\circ}\text{C}$ (Instituto Nacional de Meteorológica, Ecuador). In this location, *Z. capensis* exist in natural and man-made humid-forest gaps, pasture and early second-growth habitat. In preliminary investigations of this population we caught birds that were either molting or breeding throughout much of the calendar year, indicating less population-level seasonality of and synchrony of life history stages than in other tropical populations studied in Costa Rica (Wolf 1969), Panama (Kalma 1970), Colombia (Miller 1961, 1962; Miller and Miller 1968), Ecuador (Moore et al. 2005), Peru (Davis 1971), and Argentina (King 1973). This population, existing in a tropical environment with low seasonality, is therefore ideal for investigating the timing of life history stages – both at a population-level and among other *Zonotrichia* populations. My dissertation focused on four major topics:

Chapter II. Male territorial responsiveness in different life history stages

When it is possible to secure resources or space by defensive behavior, territorial behavior is highly advantageous (Brown 1964). Territorial behavior can be critical for the defense of: 1) paternity, 2) space used to attract and keep mates and/ or 3) space used to provide food for offspring and mates (Brown 1964; Both & Visser 2003). *The main objective of chapter two was to investigate the function of territorial behavior in the focal population by testing for differences in the territorial responses of individual male Z. capensis during different life history stages.*

Chapter III. Paternal care versus aggression

Biparental care is more common in birds than in any other vertebrate class (Clutton-Brock 1991). However, the degree of parental care provided by each sex depends on sex-specific fitness costs and benefits (Trivers 1974; Smith 1977; Clutton-Brock 1991). Males typically invest less initially into reproduction and are thus more likely to trade-off time and energy invested into paternal care for alternative activities, especially in tropical environments where clutch size is low and development is slow (Trivers 1974; Smith 1977). In tropical *Z. capensis*, biparental care is typical, but notably more care is provided by females than males (Miller & Miller 1968). *My main objective in chapter three was to investigate trade-offs between paternal care and aggression in males within the focal population of Z. capensis.*

Chapter IV. Tropical slow pace of life and response to food supplementation

The availability of food greatly influences fecundity and reproductive timing (Lack 1954; Perrins 1970; Murton & Westwood 1977; Daan et al. 1986; Wingfield & Kenagy 1991; Nagy & Holmes 2005). Recent meta-analyses suggest that the degree of reproductive advancement in response to supplemental food is greater in tropical birds than in temperate-zone breeding birds because of the lack of temporal constraint on seasonality (Schoech et al. 2008; Schoech & Hahn 2007).

However, only one experimental supplementation study has been conducted on a tropical bird (Scheuerlein and Gwinner 2002) and tropical vertebrates typically exhibit a ‘slow pace of life’ syndrome relative to their higher latitude counterparts, where resources may be better invested in maintenance and survival rather than into immediate reproduction (Ricklefs & Wikelski 2002).

The main objective of chapter four was to examine how augmented food resources provided during different life history stages are invested (e.g., into maintenance via molt or immediate reproduction) within pairs of birds in the focal population of Z. capensis.

Chapter V. Reproductive synchrony and seasonality of life history stages

Less profound seasonal variation in temperature and rainfall in humid tropical environments may permit higher variability in the timing of life history stages, possibly resulting in less population-level seasonality and synchrony of reproduction (Stutchbury & Morton 2001). However, the life history of most resident tropical species is poorly understood, making latitudinal comparisons of life history strategies difficult (Martin 1996). *The main objective of the fifth chapter was to quantify the timing of life history stages at both a population and individual level in Las Caucheras, Ecuador and to compare data on the seasonality and reproductive synchrony of the focal population with Zonotrichia populations spanning a range of latitudes and altitudes (total of two equatorial Z. capensis populations and two temperate-zone Z. leucophrys populations).*

Conclusions

My studies have clarified some aspects of seasonality in a tropical bird. In summary, *Z. capensis* do not appear to maintain a seasonal schedule based off of an annual cycle in the external environment, contrary to most temperate-zone breeding *Zonotrichia* populations. Male territorial aggression behavior peaks during periods of paternity defense (prior to breeding) and while males are defending resources needed to rearing young in the nest, similar to temperate-zone

Zonotrichia. However, unlike temperate-zone *Zonotrichia* that breed in one period of the year, territorial aggression depends on the life history stage of a given male (and the territorial pair) and is not synchronized at the level of the population. In another study, results showed male paternal care is critical to the size of fledged nestlings, which could increase offspring fitness. However, trade-offs that may exist between time allotted to territorial defense and paternal care are complex and indirect, suggesting that very different selective forces are acting in the focal tropical population than those influencing temperate-zone congeners. We also found that augmented food supply via food supplements can speed the time spent transitioning from one life history stage to another, promoting molting or breeding depending on individual history and physical condition, whereas the majority of temperate-zone bird species receiving food supplements advance the initiation of breeding in response to augmented food supply. Finally, the reproductive synchrony of tropical and temperate-zone *Zonotrichia* can be similar, though breeding at high altitude and high latitude may act in concert to influence higher reproductive synchrony to a much greater degree than breeding at high altitude in tropical latitudes. Thus, some of my studies corroborate previous studies of behavior in tropical birds, while others demonstrated results comparable to temperate-zone congeners.

Literature Cited

- Aparicio, J. M. & Bonal, R. 2002 Effects of food supplementation and habitat selection on timing of Lesser Kestrel breeding. *Ecology* **83**, 873-877.
- Aschoff, J. 1980 Biological clocks. In *Proceedings of the 17th International Ornithological Congress*, pp. 113-136. Berlin.
- Ball, G. F. 1993 The neural integration of environmental information by seasonally breeding birds. *American Zoologist* **33**, 185-199.
- Beebe, K., Bentley, G. E. & Hau, M. 2005 A seasonally breeding tropical bird lacks absolute photorefractoriness in the wild, despite high photoperiodic sensitivity. *Functional Ecology* **19**, 505-512.
- Bent, A. C. 1968 The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific Seaboard: environment and annual cycle. *University of California Publication of Zoology* **46**, 1-176.

- Blanchard, B. D. 1941 The white-crowned sparrows, *Zonotrichia leucophrys*, of the Pacific Seaboard: environment and annual cycle. *University of California Publications in Zoology* **46**, 1-178.
- Boag, P. T. & Grant, P. R. 1984 Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecological Monographs* **54**, 463-489.
- Both, C. & Visser, M. E. 2003 Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *The American Naturalist* **161**, 326-336.
- Brown, G. P., Shine, R. & Madsen, T. 2002 Responses of three sympatric snake species to tropical seasonality in northern Australia. *Journal of Tropical Ecology* **18**, 549-568.
- Brown, J. L. 1964 The evolution of diversity in avian territorial systems *The Wilson Bulletin* **76**, 160-169.
- Buehler, D. M. & Piersma, T. 2008 Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 247-266.
- Chandola-Saklani, A., Thapliyal, A., Negi, K., Diyundi, S. C. & Choudhary, B. 2004 Daily Increments of Light Hours Near Vernal Equinox Synchronize Circannual Testicular Cycle of Tropical Spotted Munia. *Chronobiology International* **21**, 553-569.
- Chapman, F. M. 1940 The post-glacial history of *Zonotrichia capensis*. *Bulletin of the American Museum of Natural History* **77**, 381-438.
- Clutton-Brock, T. H. 1991 *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Cockrem, J. F. 1995 Timing of seasonal breeding in birds, with particular reference to New Zealand birds. *Reproduction, Fertility and Development* **7**, 1-19.
- Colwell, R. K. 1974 Predictability, constancy, and contingency of periodic phenomena. *Ecology* **55**, 1148-1153.
- Daan, S., Dijkstra, C., Drent, R. & Meijer, T. 1986 Food supply and the annual timing of avian reproduction. *Acta International Ornithological Congress* **19**, 392-407.
- Davis, J. 1971 Breeding and molt schedules of the rufous-collared sparrow in coastal Peru. *The Condor* **73**, 127-146.

- Dawson, A. 2007 Seasonality in a temperate zone bird can be entrained by near equatorial photoperiods. *Proceedings of the Royal Society of London Series B-Biological Sciences* **274**, 721-725.
- Dawson, A. 2008 Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 1621-1633.
- Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. 2001 Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* **16**, 365-380.
- Deviche, P. & Sharp, P. J. 2001 Reproductive endocrinology of a free-living, opportunistically breeding passerine (white-winged crossbill, *Loxia leucoptera*). *General and Comparative Endocrinology* **123**, 268-279.
- Dittami, J. P. & Gwinner, E. 1985 Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *Journal of Zoology, London* **207**, 357-370.
- Dittami, J. P. & Gwinner, E. 1990 Endocrine correlates of seasonal reproduction and territorial behavior in some tropical passerines. In *Endocrinology of Birds: Molecular to Behavioral* (ed. M. Wada, S. Ishii & C. G. Scanes), pp. 225-233. Tokyo: Japanese Scientific Society Press.
- Emerson, S. B. & Hess, D. L. 1996 The role of androgens in opportunistic breeding, tropical frogs. *General and Comparative Endocrinology* **103**, 220-230.
- Farner, D. S. & Gwinner, E. 1980 Periodicity, circannual and reproductive cycles. In *Avian Endocrinology* (ed. A. Epplé & M. H. Stetson), pp. 331-366. New York: Academic Press.
- Goodson, J. L., Saldanha, C. J., Hahn, T. P. & Soma, K. K. 2005 Recent advances in behavioral neuroendocrinology: Insights from studies on birds. *Hormones and Behavior* **48**, 461-473.
- Gwinner, E. 1996 Circannual clocks in avian reproduction and migration. *Ibis* **138**, 47-63.
- Gwinner, E. & Dittami, J. P. 1990 Endogenous reproductive rhythms in a tropical bird. *Science* **249**, 906-908.
- Hahn, T. P. 1995 Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostra* (Aves, Carduelinae). *Journal of Experimental Zoology* **272**, 213-226.

- Hahn, T. P. 1998 Reproductive seasonality in an opportunistic breeder, the red crossbill, *Loxia curvirostra*. *Ecology* **79**, 2365-2375.
- Hahn, T. P. & MacDougall-Shackleton, S. A. 2008 Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 267-286.
- Hahn, T. P., Swingle, J., Wingfield, J. C. & Ramenofsky, M. 1992 Adjustments of the prebasic molt schedule in birds. *Ornis Scandinavica* **23**, 314-321.
- Hahn, T. P., Wingfield, J. C. & Mullen, R. 1995 Endocrine bases of spatial and temporal opportunism in arctic-breeding birds. *American Zoologist* **35**, 259-273.
- Hamner, W. H. & Stocking, J. 1970 Why don't bobolinks need Brazil? *Ecology* **51**, 743-751.
- Hau, M. 2001 Timing of breeding in variable environments: Tropical birds as model systems. *Hormones and Behavior* **40**, 281-290.
- Hau, M., Perfito, N., Moore, I.T. 2008 Timing of breeding in tropical birds: Mechanisms and evolutionary implications. *Ornitologia Neotropical* **19 (Suppl.)**, 39-59.
- Hau, M., Wikelski, M., Gwinner, H. & Gwinner, E. 2004 Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* **106**, 489-500.
- Hau, M., Wikelski, M. & Wingfield, J. C. 1998 A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 89-95.
- Hau, M., Wikelski, M. & Wingfield, J. C. 2000 Visual and nutritional food cues fine-tune timing of reproduction in a neotropical rainforest bird. *Journal of Experimental Zoology* **286**, 494-504.
- Helm, B., Schwabl, I. & Gwinner, E. 2009 Circannual basis of geographically distinct bird schedules *The Journal of Experimental Biology* **212**, 1259-1269.
- Helm, B., Piersma, T. & Van der Jeugd, H. 2006 Sociable schedules: interplay between avian social and seasonal behavior. *Animal Behaviour* **72**, 245-262.
- Illera, J. C. & Díaz, M. 2006 Reproduction in an endemic bird of a semiarid island: a food-mediated process. *Journal of Avian Biology* **37**, 447-456.
- Jacobs, J. D. & Wingfield, J. C. 2000 Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* **102**, 35-51.

- Kalma, D. L. 1970 Some aspects of the breeding ecology and annual cycle of three populations of the rufous-collared sparrow (*Zonotrichia capensis*) in Western Panama, pp. 218. New Haven: Yale.
- King, J. R. 1973 The annual cycle of the rufous-collared sparrow (*Zonotrichia capensis*) in three biotopes in northwestern Argentina. *Journal of Zoology, London* **170**, 163-188.
- King, J. R., Follett, B. K., Farner, D. S. & Morton, M. C. 1966 Annual gonadal cycles and pituitary gonadotropins in *Zonotrichia leucophrys gambelii*. *The Condor* **68**, 476-487.
- Komdeur, J. 1996 Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: a field experiment using translocation. *Journal of Biological Rhythms* **11**, 333-346.
- Komdeur, J. & Daan, S. 2005 Breeding in the monsoon: semi-annual reproduction in the Seychelles warbler (*Acrocephalus sechellensis*). *Journal of ornithology* **146**, 305-313.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Lambrechts, M. M., Perret, P. & Blondel, J. 1996 Adaptive differences in the timing of egg laying between different population of birds results from variation in photoresponsiveness. *Proceedings of the Royal Society B* **263**, 19-22.
- Lofts, B. 1964 Evidence of an autonomous reproductive rhythm in an equatorial bird (*Quelea quelea*). *Nature* **201**, 523-524.
- Lofts, B. & Murton, R. K. 1968 Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *Journal of Zoology, London* **155**, 327-394.
- Marshall, A. J. 1970 Environmental factors other than light involved in the control of sexual cycles in birds and mammals. In *La Photoregulation de la Reproduction Chez les Oiseaux et les Mammiferes*. (ed. J. Benoit & I. Assenmacher), pp. 53-64. Paris: Presses du CNRS.
- Martin, T. E. 1996 Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**, 263-272.
- Menaker, M. 2006 Circadian organization in the real world. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 3015-3016.
- Miller, A. H. 1959a Reproductive cycles in an equatorial sparrow. *PNAS* **45**, 1095-1100.

- Miller, A. H. 1959b Response to experimental light increments by Andean sparrows from an equatorial area. *The Condor* **61**, 344-347.
- Miller, A. H. 1961 Molt cycles in equatorial Andean sparrows. *The Condor* **63**, 143-161.
- Miller, A. H. 1962 Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **48**, 396-400.
- Miller, A. H. 1965 Capacity for photoperiodic response and endogenous factors in the reproductive cycles of an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **54**, 97-101.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, I. T., Bonier, F. & Wingfield, J. C. 2005 Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology* **16**, 755-762.
- Moore, M. C. 1983 Effect of female sexual displays on the endocrine physiology and behaviour of male white-crowned sparrows, *Zonotrichia leucophrys*. *Journal of the Zoological Society of London* **199**, 137-148.
- Morton, M. L. 1978 Snow conditions and the onset of breeding in the mountain white-crowned sparrow *Condor* **80**, 285-289.
- Morton, M. L. (ed.) 2002 *The mountain white-crowned sparrow: migration and reproduction at high altitude*. Cooper Ornithological Society Publication, Allen Press, Lawrence. Lawrence: Allen Press.
- Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford, U. K.: Clarendon Press.
- Nagy, L. R. & Holmes, R. T. 2005 Food limits annual fecundity of a migratory songbird: An experimental study. *Ecology* **86**, 675-681.
- Novoa, F. F., Veloso, C. & López-Calleja, M. V. 1996 Seasonal changes in diet, digestive morphology and digestive efficiency in the rufous-collared sparrow (*Zonotrichia capensis*) in central Chile. *The Condor* **98**, 873-876.
- Paul, M. J., Zucker, I. & Schwartz, W. J. 2008 Tracking the seasons: the internal calendars of vertebrates. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 341-361.

- Perfito, N., Kwong, J. M. Y., Bentley, G. E. & Hau, M. 2008 Cue hierarchies and testicular development: Is food a more potent stimulus than day length in an opportunistic breeder (*Taeniopygia g. guttata*)? *Hormones and Behavior* **53**, 567-572.
- Perfito, N., Ubuka, T., Zann, R. A., Hau, M. & Bentley, G. E. 2006 Opportunism at work: regulation of the reproductive axis in wild populations of zebra finches. *Integrative and Comparative Biology* **46**, E109-E109.
- Perfito, N., Zann, R. A., Bentley, G. E. & Hau, M. 2007 Opportunism at work: habitat predictability affects reproductive readiness in free-living zebra finches. *Functional Ecology* **21**, 291-301.
- Perrins, C. M. 1970 The timing of birds' breeding seasons. *Ibis* **112**, 242-255.
- Ricklefs, R. E. & Wikelski, M. 2002 The physiology/ life-history nexus. *Trends in Ecology & Evolution* **17**, 462-468.
- Scheuerlein, A. & Gwinner, E. 2002 Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. *Journal of Biological Rhythms* **17**, 171-180.
- Schoech, S. J. 1996 The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay. *Condor* **98**, 234-244.
- Schoech, S. J., Bowman, R. & Reynolds, S. J. 2004 Food supplementation and possible mechanisms underlying early breeding in the Florida Scrub-Jay (*Aphelocoma coerulescens*). *Hormones and Behavior* **46**, 565-573.
- Schoech, S. J., Bridge, E. S., Boughton, R. K., Reynolds, S. J., Atwell, J. W. & Bowman, R. 2008 Food supplementation: A tool to increase reproductive output. A case study in the threatened Florida Scrub-Jay. *Biological Conservation* **141**, 162-173.
- Schoech, S. J. & Hahn, T. P. 2005 Timing of reproduction and food supplementation: Are high latitude species less responsive than low latitude to non-photic cues? *Integrative and Comparative Biology* **45**, 1069-1069.
- Schoech, S. J. & Hahn, T. P. 2007 Food supplementation and timing of reproduction: does the responsiveness to supplementary information vary with latitude? *Journal of Ornithology* **148**, S625-S632.
- Schoech, S. J. & Hahn, T. P. 2008 Latitude affects degree of advancement in laying by birds in response to food supplementation: a meta-analysis. *Oecologia* **157**, 369-376.

- Small, T. W. & Moore, I. T. 2009 Seasonal neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding birds. *General and Comparative Endocrinology* **163**, 135-141.
- Smith, J. M. 1977 Parental investment: a prospective analysis. *Animal Behaviour* **25**, 1-9.
- Strand, C. R., Small, T. W. & Deviche, P. 2007 Plasticity of the Rufous-winged Sparrow, *Aimophila carpalis*, song control regions during the monsoon-associated summer breeding period. *Hormones and Behavior* **52**, 401-408.
- Stutchbury, B. J. M. & Morton, E. S. 2001 *Behavioral Ecology of Tropical Birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- Trivers, R. L. 1974 Parent-offspring conflict *American Zoologist* **14**, 249-264.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. & Holmes, R. T. 2002 Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* **17**, 76-83.
- Wikelski, M., Hau, M., Robinson, W. D. & Wingfield, J. C. 2003 Reproductive seasonality of seven neotropical passerine species. *Condor* **105**, 683-695.
- Wikelski, M., Hau, M. & Wingfield, J. C. 2000 Seasonality of reproduction in a neotropical rain forest bird. *Ecology* **81**, 2458-2472.
- Wikelski, M., Martin, L. B., Scheuerlein, A., Robinson, M. T., Robinson, N. D., Heim, B., Hau, M. & Gwinner, E. 2008 Avian circannual clocks: adaptive significance and possible involvement of energy turnover in their proximate control. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 411-423.
- Wilson, E. O. 1999 *The Diversity of Life*. New York, NY: Norton and Company.
- Wingfield, J. C. 2005 Flexibility in annual cycles of birds: implications for endocrine control mechanisms. *Journal of ornithology* **146**, 291-304.
- Wingfield, J. C. 2008 Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 425-441.

- Wingfield, J. C. & Farner, D. S. 1978 The endocrinology of a natural breeding population of the white-crowned sparrow (*Zonotrichia leucophrys pugetensis*). *Physiological Zoology* **51**, 188-205.
- Wingfield, J. C. & Farner, D. S. 1980 Environmental and endocrine control of seasonal reproduction in temperate zone birds. *Progress in Reproductive Biology* **5**, 62-101.
- Wingfield, J. C., Hahn, T. P., Levin, R. & Honey, P. 1992 Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology* **261**, 214-231.
- Wingfield, J. C., Hahn, T. P., Wada, M., Astheimer, L. B. & Schoech, S. 1996 Interrelationship of day length and temperature on the control of gonadal development, body mass, and fat score in white-crowned sparrows, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology* **101**, 242-255.
- Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S. L., Maney, D. L. & Soma, K. K. 2000 Toward an ecological basis of hormone-behavior interactions in reproduction of birds. In *Reproduction in Context. Social and Environmental Influences on Reproduction* (ed. K. Wallen & J. E. Schneider), pp. 85-128. Cambridge, MA, London: A Bradford Book, The MIT Press.
- Wingfield, J. C. & Kenagy, G. J. 1991 Natural regulation of reproductive cycles. In *Vertebrate Endocrinology: Fundamentals and Biomedical Implications*, vol. 4 (ed. P. K. T. Pawg & M. P. Schreibruan), pp. 181-241. San Diego: Academic Press, Inc.
- Wingfield, J. C. & Moore, M. C. 1987 Hormonal, social, and environmental factors in the reproductive biology of free-living male birds. In *Psychobiology of Reproductive Behavior: and Evolutionary Perspective* (ed. D. Crews), pp. 149-175. New Jersey: Prentice Hall.
- Wolf, L. L. 1969 Breeding and molting periods in a Costa Rican population of the Andean sparrow. *The Condor* **71**, 212-219.
- Zink, R. M. & Blackwell, R. C. 1996 Patterns of allozyme mitochondrial DNA, and morphometric variation in four sparrow genera. *The Auk* **113**, 59-67.

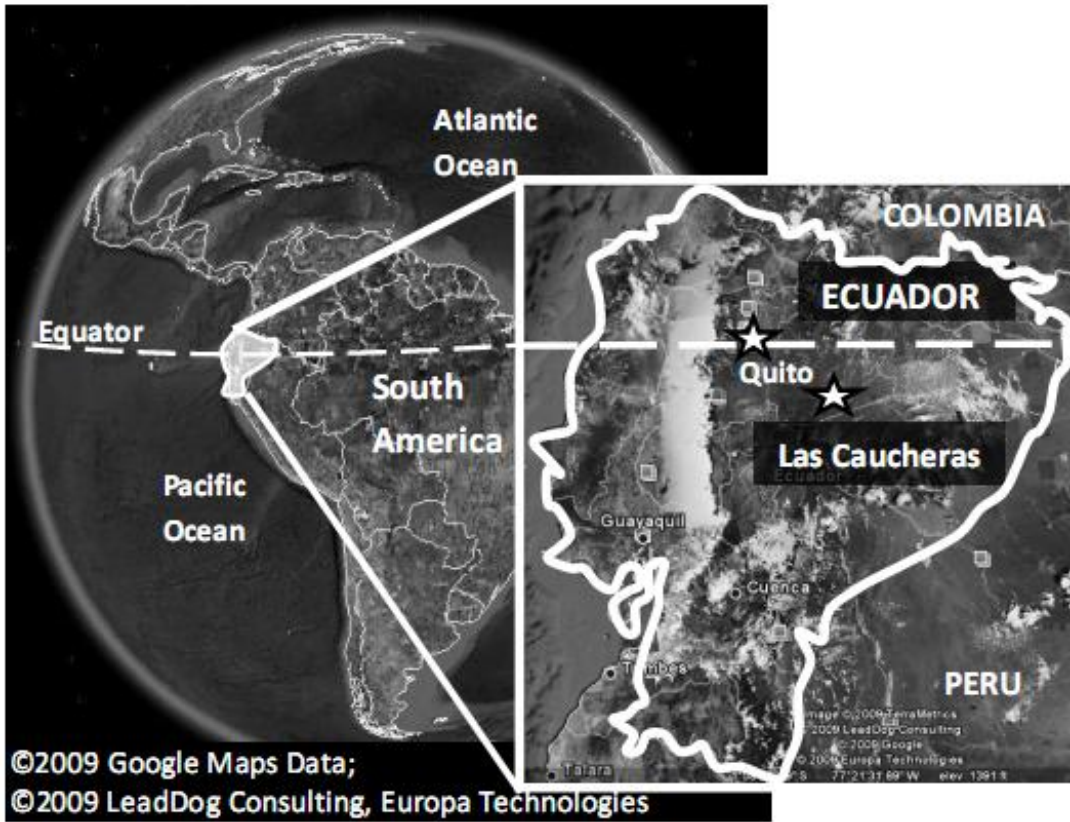


Figure 1.1 Satellite map of the Las Caucheras study site in Ecuador, South America.

CHAPTER II. TERRITORIAL AGGRESSION IN TROPICAL RESIDENT RUFOUS-COLLARED SPARROWS (*ZONOTRICHIA CAPENSIS*)

Alexandra M. Class and Ignacio T. Moore

Abstract

Territorial defense evolves where resources are defensible and where resource defense secures a fitness advantage. However, territorial defence can involve substantial energetic and survival costs, particularly in species that defend territories year-round. Year-round territory defense is common in tropical bird species and, in conjunction with the lower seasonality of tropical environments, provides an opportunity to test the function of territoriality. Three different forces are considered to select for territorial aggression: paternity protection, mate attraction and/or food resource defense. We tested the function of male territorial aggression across life history stages in a resident population of equatorial rufous-collared sparrows (*Zonotrichia capensis*) in the humid eastern Andes of Ecuador across life history stages. Simultaneously, we examined the synchrony of life history stages at the population-level. Individuals were identified and classified into one of five life history stages: pre-breeding, nesting, feeding fledglings (young out of the nest), molting (replacing feathers), or non-breeding. To determine male aggressiveness, we performed simulated territorial intrusions with a mounted decoy. Males were significantly more aggressive during pre-breeding and nesting than while feeding fledglings, molting, or in non-breeding. We found individuals within the population in all life history stages during the sampling periods, demonstrating population-level asynchrony. Therefore, individual males in this population defend territories according to life history stage, not according to environmental season. Based on these results, we suggest that the selective forces of mate attraction and paternity protection may best explain the territorial aggression pattern observed.

Introduction

Seasonality of behavior, particularly reproduction, has been well described in animals from temperate latitudes (reproduction; Murton & Westwood 1977; Wingfield & Kenagy 1991). The temperate latitude environment (latitudes north of the Tropic of Cancer and south of the Tropic of Capricorn, 23° 26'N or S, respectively) is dominated by changes in photoperiod, which are primarily responsible for climatic differences between winter and summer seasons. At higher latitudes, increasing photoperiod is used to predict the arrival of favorable climate and resources and to coordinate energetically demanding life history stages, such as breeding and migration, with favorable climate and abundant food resources (reviewed in Murton & Westwood 1977; Wingfield & Kenagy 1991). In studies of behavioral seasonality in animals, the focus of research is typically reproductive seasonality, and the majority of animals breed when food abundance is high (e.g., spring or summer) (Murton & Westwood 1977; Wingfield & Kenagy 1991; Hahn & Schoech 2008). Other behaviors, such as migration or molt, are also seasonal and generally timed around reproduction (Jacobs & Wingfield 2000; Dawson 2006; Wikelski et al. 2008). Because of the reliance on photoperiod as a global-scale predictive environmental cue, populations at similar latitudes tend to time seasonal behaviors to similar times of the year (Martin et al., in review).

Many tropical environments are seasonal even though daily change in photoperiod is low in tropical latitudes (Bronson & Heideman 1992; Stutchbury & Morton 2001; Shine & Brown 2008). Non-photoperiodic cues such as predictable seasonal rainfall (e.g., Crook 1960, 1963, 1964; Brown & Shine 2002; Hau et al. 2004), or seasonal food availability (e.g., Dinerstein 1986; van Schaik et al. 1993; Scheuerlein & Gwinner 2002; Hockey & Wilson 2003; Perfito et al. 2008) may therefore be more important in determining the timing of life history stages in tropical latitudes (Hau et al. 2001; Hahn & MacDougall-Shakleton 2008). While we still do not know the timing of most tropical species' life history stages, seasonal reproduction appears to be common among tropical species studied to date (birds: Baker 1938; Skutch 1950; Ricklefs 1966; Sinclair 1978; Hau et al. 1998; Wikelski et al. 2003; reptiles: Saint-Girons 1982; Hartmann et al. 2002; Shine & Brown 2008; mammals: Bronson & Heideman 1992; O'Brian 1993; Cumming & Bernard 1997). However, our understanding of tropical life histories remains limited by a bias toward investigations of reproductive behavior rather than non-reproductive behavior or behavior associated with reproduction (e.g., territorial behavior) (Stutchbury & Morton 2001).

Territorial behaviors evolve where resources are defendable and where the defense of resources secures a reproductive advantage (Brown 1964). Though territorial behaviors can be costly in terms of increased energy expenditure and predation risk associated with active displays, the costs are considered to be outweighed by the advantage gained by defending a territory in populations exhibiting territoriality (Moore & Marler 1987; Marler & Moore 1988; Wingfield et al. 1990; Wingfield et al. 2001; Dunn et al. 2004). Three principal selective forces are hypothesized to influence territorial aggression defense: 1) paternity protection, where territorial defense is primarily aimed against conspecific male intruders because of the potential paternity threat of extra-pair fertilizations, 2) food resource defense, where territories are defended because they provide necessary food resources for mates and young and/or (3) mate attraction, where territorial defense secures a territory space to attract and secure a mate(s) (Brown 1964). These categories are not necessarily mutually exclusive (Brown 1964).

The selective forces of paternity protection, food resource defense and mate attraction each predict distinct patterns of territorial aggression across life history stages. Paternity protection predicts that males will show peak levels of territorial aggression during pre-breeding (when mates are fertile, but clutches have not been laid) periods when their mates are fertile and the threat of cuckoldry by extra-pair males is high. Food resource defense predicts that males will show peak territorial aggression during nesting periods, when defense of food resources on their territory may greatly improve their ability to provision young and/ or mates (e.g., when there are nests with immobile young). Mate attraction predicts individual males will have high territorial aggression responses during periods when they establish and defend territory spaces to attract and/ or keep mates.

In temperate latitude breeding birds, most species defend a territory during the pre-breeding and nesting season, when the climate is benign and conditions are suitable to rear young (~90% of temperate species; Stutchbury & Morton 2001). Mate attraction is considered to be a strong selective force on male territorial aggression in birds breeding in the temperate-zone. For example, many migratory temperate-zone breeding birds return to their breeding grounds from their wintering grounds and immediately engage in fierce competition for territories prior to attracting a mate and breeding (Brown 1964; Murton & Westwood 1977; Wingfield & Moore 1987). Paternity protection is also likely to influence high territorial aggression during the pre-breeding season in temperate-zone territorial birds, as extra-pair paternity is high (Brown 1964;

Wingfield & Moore 1987; Weatherhead & Yezerinac 1998; Kokko 1999; Griffith et al. 2002; Kokko et al. 2006; Stutchbury & Morton 2008). However, territorial aggression responses and the hormones that control territorial aggression decline as birds move from fertile periods to feeding young, because of potential negative consequences of misplaced territorial aggression behavior (Wingfield & Moore 1987). In the temperate-zone territorial defense of food resources may be selectively advantageous while young are in the nest and pairs are therefore closely tied to their territories, as it supports successful reproduction and higher survival of offspring to have higher food availability in close proximity to the nest (Hogstedt 1980; Svensson & Nilsson 1995; Pribil & Searcy 2001).

In contrast to temperate-zone breeding birds, tropical birds have evolved a diversity of territorial systems, potentially associated with a less climatically seasonal environment (Stutchbury & Morton 2001). Year-round, all-purpose territorial defense is the most common type of territoriality reported for tropical bird species (Stutchbury & Morton 2001). Year-round all-purpose territoriality is thought to be advantageous where optimal habitat or a necessary resource is always limited (Brown 1964; Stutchbury & Morton 2001). In such a situation, a particular resource, such as a high quality nesting space, may be difficult or impossible to acquire without a territory, but critical to attract and keep mate(s) (Brown 1964; Smith 1978). Few studies have examined the territoriality of tropical species outside of breeding seasons. Thus, the question remains whether year-round resident tropical bird species simply reside on their territories or actively defend territories across all life history stages.

The behavioral ecology of our focal species, the rufous-collared sparrow (*Zonotrichia capensis*) is well-studied compared with most tropical species, although studies have concentrated on their reproductive ecology. *Zonotrichia capensis* is distributed from Chiapas, Mexico to Tierra del Fuego, Argentina (0 m - 3500 m altitude) and is the only tropical member of its genus. *Zonotrichia capensis* is a socially monogamous, omnivorous, emberizid sparrow that is a year-round resident with non-obligatory biparental care (Miller & Miller 1968; Kalma 1970; King 1973). Male *Z. capensis* are primarily responsible for the defense of territories (Busch et al. 2004, Moore et al. 2004). Female *Z. capensis* typically provide more care to offspring than males (Miller & Miller 1968, Kalma 1970). *Zonotrichia capensis* are not necessarily restricted to their territory boundaries while foraging, and older fledged young leave territories to forage with more frequency as they reach independence (Miller & Miller 1968;

Wolf 1969; Davis 1971). Monogamous pairs of *Z. capensis* may remain together for life (up to 9 years) (Moore unpub. data). However, environmental disturbance, socially-mediated divorce, or death can prompt re-pairing (Miller 1962; Miller & Miller 1968). Seasonal reproduction has been documented in populations of *Z. capensis* in Costa Rica (Wolf 1969), Panama (Kalma 1970), Colombia (Miller 1959; Miller & Miller 1968), Ecuador (Moore et al. 2005), Peru (Davis 1971), and Argentina (King 1973). Yet, the timing and duration of breeding seasons varies considerably across the latitudinal and altitudinal range of *Z. capensis*. In some populations of *Z. capensis*, pairs have been observed breeding two times per year, but not necessarily on a predictable annual seasonal schedule (Miller & Miller 1968; Kalma 1970; Davis 1971; King 1973; Class unpub. data). For example, Miller (1959, 1962) reported that most individuals breed at approximately 6 month intervals in the Colombian Andes (~2000 m). However, in a high altitude (3300 m) population in Papallacta, Ecuador, most individuals breed during a 3-month breeding season from September-November (Moore et al. 2005). Preliminary data from the Papallacta population (3300 m) reveal that extra-pair paternity does occur, with rates similar to temperate latitude breeding *Zonotrichia* populations (Bonier unpub. data).

Previous studies focusing on territorial aggression and reproductive physiology in high altitude populations of *Z. capensis* in Ecuador reported high levels of territorial aggression and reproductive hormones during the pre-breeding life history stage, similar to temperate *Zonotrichia* (Moore et al. 2002; Busch et al. 2004; Moore et al. 2004a; Moore et al. 2004b; Moore et al. 2005). However, no study has tested how territorial aggressive behavior varies across adult life history stages in tropical environments with low seasonality. Here we test the function of territorial aggression across different life history stages in a resident population of *Z. capensis* in the humid eastern Andes of Ecuador at mid-altitude (2100 m altitude), where there is markedly less climatic seasonality than previously studied equatorial populations (i.e., populations at 2900 m and 3300 m, Moore et al. 2005; Miller & Miller 1968; Davis 1971; A. M. Class unpub. data).

In this tropical year-round resident population the hypothesized selective forces of paternity protection, food resource defense and mate attraction make specific predictions for high territorial aggression. If paternity protection is at work in the focal population we predict that territorial aggression should peak during pre-breeding, when the threat of covert copulations is high. If food resource defense is a major selective force in the focal population we predict that

there will be peak territorial aggression during nesting, when pairs must feed young in nests on the territory. If the selective force of mate attraction is acting primarily, we predict that high levels of territorial aggression occur year-round (to attract and keep a mate via defense of territory space). As part of this study, we also show evidence for the low synchrony of life history stages in the study population. Low synchrony of life history stages in the study population provides an opportunity to separate the possible functions of territoriality in the absence of seasonal influences on selective forces that complicate investigations of temperate-zone territorial systems.

Methods

Study population and life history stages

The study population of *Z. capensis* is located in the rural township of Las Caucheras in Napo Province of eastern Andes of Ecuador (0°36'S, 77°54'W; altitude ~2100 m). *Zonotrichia capensis* inhabits natural gaps, pasture, and early second-growth habitat. Though there is consistent high rainfall (~2500 - 3500 mm per yr), monthly accumulated rainfall is between 130 - 240 mm from October - March and 280-390 mm from April - September (Instituto Nacional de Meteorología, Ecuador). Mean monthly air temperature remains nearly constant throughout the year at this site (~17° C, Instituto Nacional de Meteorología, Ecuador). Daily photoperiod varies minimally over the course of the year at this site, similar to previously studied sites at similar equatorial latitudes (e.g., for Papallacta, Ecuador: Bendix & Rafiqpoor 2001; Moore et al. 2005).

Birds were caught using mist nets. In addition to daily passive mist-netting, we actively targeted mist-netting toward specific territorial residents (see below). Each bird received a unique combination of color bands and a numbered aluminum band. Measurements of reproductive morphology, molt (periodic loss and replacement of feathers) scores and behavioral observations were used to categorize individuals as belonging to one of five life history stages: pre-breeding, nesting, feeding fledglings, molting and non-breeding (see Table 2.1). Reproductive morphology included evaluating the brood patch (developed to brood eggs and young) for females, and length and width of the cloacal protuberance (an extension of the cloaca used to deposit sperm during copulation) for males. Cloacal protuberance size closely tracks testis volume in this species (Moore et al. 2005). We defined five brood patch stages in females:

1) defeathering, 2) defeathered, 3) edematous with hyperplastic epidermis (fluid-filled distended skin pouch used for incubation), 4) refeathering, wrinkled/scaly skin, and 5) nearly refeathered (about 10% sheathed, regrowing feathers; scaly skin may still be visible). We made additional observations of behavior on all territories over several days, both before and after conducting simulated territorial intrusions (STIs), to verify that life history stages were assigned accurately.

Definition of territories and simulated territorial intrusion protocol

In both sampling periods, 16 March – 10 June and 6 September – 3 December, 2007, we identified, observed and captured territorial residents to determine their life history stage. During observational periods of one or more hours, we noted the frequency of use of specific landmarks (such as bushes, logs and trees) by focal males while they were singing, foraging, and perching. Landmarks and areas most frequently occupied by the residents were used as guide to approximate territory boundaries and central areas, in which we placed the decoy and playback equipment for STIs. We attempted STIs only when territories and life history stage were determined and when weather permitted.

We conducted each STI on a unique male. All STIs occurred between 1200 and 1800 hrs. While both live and stuffed decoy types have been used in STI experiments, a recent study suggested that stuffed decoys can illicit stronger aggressive responses (Scriba & Goymann 2008) and in initial STI trials we observed no difference in male responses to live or stuffed decoys. Therefore, we used three stuffed decoys from the study population, mounted on a stick, for all STIs. We paced out a 5 m radius around the territory center a day prior to each STI to ensure more accurate estimates of distance and time. Immediately prior to each experiment, we placed the decoy and song playback equipment in the defined territory center, after focal males were located visually. During the experiments, we stood at least 15 m from the territory center, a distance at which we were presumably not perceived as a threat (i.e., no chipping/flights directed to the observer).

Each STI consisted of three consecutive 10 min observation periods. In the first 10 min of the observation period (min 0 - 10), the decoy was covered and there was no song playback. This period determined background levels of territorial aggression. After this initial 10 min period, we uncovered the decoy and started a song playback track that ran for the next 10 min period of observation. This period corresponded to active territorial defense. For each STI we selected a

single song for playback from 12 song tracks recorded from 12 different males in 2006. None of the recorded males were subjects of STI experiments described here. Each track had a single, randomly selected song (to avoid pseudoreplication; Kroodsma et al. 2001), followed by 9 seconds of silence, to approximate the natural song rate of *Z. capensis* in this population. Song playback and STI procedures were similar to methods used in previous studies of *Z. capensis* (Busch et al. 2004; Moore et al. 2004a). Playback volume simulated normal ranges of observed song volume, adjusted for locale. For the third 10 min observation period (min 20 - 30), we recovered the decoy and turned off the song playback. During all three periods, we recorded the duration of time the focal male was within 5 m of the decoy, his closest approach to the decoy (m), number of attacks, number of songs, number of song switches (number of times each bird used a different song type) and number of flights. During the STI period (min 10 - 20), we also recorded latency, or the time elapsed, until the male responded to the intruder. During the post-STI (min 20 - 30) we recorded the persistence of aggressive response (the time the male continued to display aggressive behavior, continued to sing, or attempted to locate the decoy, despite the disappearance of the threat).

Data analyses

To compare territorial aggression across life history stages and among STI periods, we generated a single aggression score (Busch et al. 2004; Moore et al. 2004a) for each of 89 males using principal components analysis (PCA). We did not observe any attacks during any STI; therefore, we did not include this among the measured behaviors in the PCA. We used the first principal component (PC1) as the aggression score for each male tested (Table 2.2). Means of PC1 scores were compared using a repeated-measures one-way ANOVA across life history stages and across STI periods (i.e., pre-STI, STI, post-STI), including interactions between life history stage and STI periods. Tukey-Kramer HSD post-hoc tests were used to identify significant differences among life history stages and among STI periods. In case the variance in some individual behaviors was masked by the PCA, we also examined individual behaviors measured among life history stages and STI periods using one-way ANOVAs. We used Tukey-Kramer HSD post-hoc tests to determine significant differences among measured behaviors in different life history stage and STI periods. The latency and persistence of aggressive responses were measured only during the STI (latency) and post-STI periods (persistence); they were each analyzed one-way

ANOVAs. Tukey-Kramer HSD post-hoc tests were used to detect where there were significant differences in latency and persistence responses among life history stages.

To examine the synchrony of life history stages within the population, we compiled all data on life history stages of identified territorial individuals. Data from the two sampling periods was further divided into approximately 30-day time periods during each of the two sampling periods. We combined the pre-breeding, nesting and feeding fledgling life history stages (though some individuals in each life history stage were observed in all sampling periods) into a general “breeding” category for simplicity of the analysis. Sampling effort in each of the two field periods was approximately equal. However, the subdivision of 30-day periods and times when we conducted STIs led to a few more (or less) territories each category.

Results

Aggression responses across life history stages

There was a significant effect of life history stage (pre-breeding, nesting, feeding fledglings, molting and non-breeding) on the male aggressive score (Fig. 2.1; repeated measures one-way ANOVA: $F_{4, 84} = 28.54, p < 0.0001$). Post-hoc analysis revealed that males in the pre-breeding and nesting life history stages were significantly more aggressive than males feeding fledglings, molting or in non-breeding (Fig. 2.1; Tukey-Kramer HSD: $p < 0.0001$). There was no difference between pre-breeding and nesting life history stages (Fig. 2.1; Tukey-Kramer HSD; $p = 0.667$), nor between the non-breeding, molting and feeding fledgling stages (Fig. 2.1; Tukey-Kramer HSD; non-breeding versus molting, $p = 0.117$; non-breeding versus feeding fledglings, $p = 0.211$; feeding fledglings versus molting, $p = 0.999$).

There was also a significant effect of the STI period on the aggression responses of males (Fig. 2.1; compare a, b, c; repeated measures one-way ANOVA: $F_{2, 168} = 145.64, p < 0.0001$). Post-hoc analysis of STI periods revealed pre-STI, STI, and post-STI periods were all significantly different from one another (Fig. 2.1; Tukey-Kramer HSD; $p < 0.0001$). There was a trend for an interaction of life history stage and STI period (repeated measures one-way ANOVA: $F_{8, 168} = 1.74, p = 0.092$).

Comparisons of individual behavioral responses

We analyzed within each STI period (pre-STI, STI, post-STI) and among life history stages for each behavior recorded from resident male *Z. capensis*. One-way ANOVA tests revealed a significant effect of life history stage in the pre-STI period for the behaviors: time spent within 5 m ($F_{4, 84} = 8.15, p < 0.0001$), closest approach (m) ($F_{4, 84} = 13.45, p < 0.0001$), number of songs ($F_{4, 84} = 9.9148, p < 0.0001$) and number of flights ($F_{4, 84} = 5.48, p = 0.0006$) (Table 2.3). There was no significant difference in the number of song-switches in the pre-STI period (one-way ANOVA: $F_{4, 84} = 0.9177, p = 0.46$). See Table 3 for Tukey-Kramer post-hoc test results). Neither latency nor persistence behaviors were relevant during the pre-STI period.

In the STI period, one-way ANOVA revealed significant differences among males in different life history stages for the behaviors: time within 5 m of the decoy ($F_{4, 84} = 12.53, p < 0.0001$), closest approach (m) ($F_{4, 84} = 7.64, p < 0.0001$) and number of songs ($F_{4, 84} = 22.09, p < 0.0001$). The one-way ANOVA revealed no significant difference in the number of song-switches ($F_{4, 84} = 1.38, p = 0.25$) nor number of flights ($F_{4, 84} = 0.52, p = 0.72$) during the STI period. There were significant differences in the latency to respond among males in different life history stages, a measure recorded only during the STI period (one-way ANOVA: $F_{4, 84} = 6.77, p < 0.0001$). See Table 3 for Tukey-Kramer post-hoc test results.

In the post-STI period, one-way ANOVA revealed significant differences among males in different life history stages for the behaviors: time within 5 m ($F_{4, 84} = 10.96, p < 0.0001$), closest approach to the decoy ($F_{4, 84} = 11.18, p < 0.0001$), number of songs ($F_{4, 84} = 18.43, p < 0.0001$), number of song-switches ($F_{4, 84} = 3.95, p = 0.006$) and number of flights ($F_{4, 84} = 3.04, p = 0.02$). There were significantly different persistence responses to the STI among males in different life history stages, a measure recorded only during the post-STI period (one-way ANOVA: $F_{4, 84} = 9.27, p < 0.0001$). See Table 2.3 for Tukey-Kramer post-hoc test results.

Synchrony of life history stages

Combining both sampling periods in 2007, we identified 92 total territories and were able to use 89 for STIs. We found and identified an equal number of territories in each sampling period ($n = 46$, Fig. 2.2). Territories in which we were unable to complete STIs (for weather-related or logistical reasons) were not included the STI analysis above, but are included in Figure 2.2, to

provide the most complete picture synchrony of life history stages possible. We found pairs in all life history stages in both sampling periods (Fig. 2.2).

Discussion

In our study, *Z. capensis* males responded more aggressively to STIs during the pre-breeding and nesting life history stages than during the feeding fledglings, molting or non-breeding life history stages. However, there was a significant aggressive response to the STI in all life history stages compared to the control periods (i.e., the pre-STI period; see Fig. 2.1a, b, c). Thus, the presence of an intruder always elicited a significant response (in comparison with background levels), regardless of the life history stage of a resident male.

Evaluating selective forces on territorial aggression

The paternity protection hypothesis predicts that territorial defense should occur primarily during pre-breeding, when females are fertile and the threat of covert extra-pair fertilization is high. Given that extra-pair fertilization are common in another population of *Z. capensis* in Ecuador, at rates comparable to highly seasonal temperate *Zonotrichia* (Bonier unpub. data), it is likely that extra-pair fertilizations are also prevalent in the focal population. We observed high aggression responses during pre-breeding, suggesting that paternity protection is an important selective force on territorial aggression. Females are fertile and capable of extra pair copulations in the pre-breeding life history stage, thus resident males must defend against any male, as males may threaten paternity (Weatherhead & Yerzerinac 1998; Kokko 1999).

In the nesting life history stage male territorial aggression responses remained high and were statistically indistinguishable from pre-breeding levels. As females are not fertile throughout nesting the threat of extra-pair fertilizations is not a viable explanation for high aggressive responses during nesting. That peak territorial aggression was statistically indistinguishable between pre-breeding and nesting life history stages suggests that the function of territorial aggression is different for individual males in Las Caucheras than in the majority of temperate-zone territorial birds. In temperate-zone birds that establish breeding territories there is a characteristic decline in aggression from pre-breeding to nesting periods. In temperate-breeding species territorial aggression, and the androgen hormones that mediate territorial aggression, are known to interfere with paternal care and potentially can lead to misplaced aggression resulting

in harm to young (Wingfield & Moore 1987). We therefore suggest that there may be a very different (or decoupled) relationship between the aggression response and the hormone(s) responsible for territorial aggression in individual males in Las Caucheras. Similarly, the relationships between androgens and aggressive behavior have been shown to be uncoupled in other populations of *Z. capensis* in Ecuador (Moore et al. 2004a, b) Given that there was a statistically indistinguishable peak in aggression during the nesting period we suggest that aggression responses during the nesting life history stage may be directed at defending food resources for young. Food resource defense predicts territorial defense will be greatest when young are in the nest and parents are closely tied to the territory to provision dependent young. In Las Caucheras individual *Z. capensis* generally gather food resources from within the territory during the nesting life history stage (Class pers. obs.).

We observed significantly lower territorial aggression responses in the feeding fledglings life history stage. During this stage, young are still dependent on parents and, according to the food resource defense hypothesis, aggression should therefore remain high. However, pairs of *Z. capensis* are not tied to territories for food resources and are observed foraging for resources outside of their territory (Miller & Miller 1968; Wolf 1969; King 1973). Additionally, older *Z. capensis* fledglings leave territory boundaries to forage in mixed-age flocks as they reach independence from adults (Miller & Miller 1968; Kalma 1970; Smith 1978). Together these observations suggest that food resource defense selects for high territorial aggression solely during the nesting life history stage.

Alternatively, high territorial aggression during nesting may be aimed at potential nest predators. Though nest predation appears to be high in other tropical *Z. capensis* populations (Miller & Miller 1962; Kalma 1970; Bonier pers. com.), in this study we tested aggressive responses to a conspecific intruder and not to potential predators. It is unlikely that territorial aggression is aimed solely at nest predators in the nesting life history stage, because there was a significant aggression response to conspecific intruders.

Year-round resident tropical birds that make use of less temporally constrained resources (e.g., tropical humid forest residents or tropical seabirds) can potentially reproduce during most or all months of the calendar year (Stonehouse 1962; Snow 1965; Ashmole 1968; Miller & Miller 1968; Kalma 1970). In these cases, competition for high quality territories is intense and year-round, in comparison to the brief period of competition for territories in temperate latitude

breeding bird species (Snow 1965; Ashmole 1968; Murton & Westwood 1977). Thus, territorial space is at a premium and territory holders are at risk of losing territories if they do not defend their territories (Snow 1965; Ashmole 1968; Smith 1978). We show that territorial defense occurs in every life history stage (e.g. the STI elicited a territorial response in all life history stages), but that territorial aggression appears to be held at a low level when the threat of cuckoldry and resource competition is low (i.e., in feeding fledglings, molting and non-breeding life history stages). Territoriality may be maintained to defend territory space and quality habitat for nesting because these resources are essential for year-round mate attraction and/ or to keep a current mate, in accordance with the mate attraction hypothesis. In this view, there is a shift from the significantly higher aggressive responses of males in the pre-breeding and nesting life history stages, directed at defense of paternity and food resources, to lower aggression levels needed to defend territory space (for mate attraction) in the feeding fledglings, molting and non-breeding life history stages.

Males in the feeding fledglings and molting life history stages face considerable temporal and energetic costs that may explain why their territorial aggression responses were significantly lower than males in other life history stages (Murphy 1996; Schieltz & Murphy 1997; Weathers et al. 2003). Males in the feeding fledgling life history stage may have low territorial aggression responses because their young are mobile and thus defense of territorial space becomes less necessary. Molting presents a substantial energetic cost that occurs over a prolonged period of 6-8 weeks in *Z. capensis* (Miller & Miller 1968), which may explain why molting birds had low aggression responses. Non-breeding birds were not tied to territories because of nests and had no obligation to feed young, thus may also have less of a need for peak territorial defense. Further support for the primary importance of defense during the pre-breeding and breeding life history stages comes from patterns in the pre-STI and post-STI responses (Fig. 2.1). High vigilance in the pre-STI period and prolonged aggression response in the post-STI period is apparent in Figure 2.1 in the pre-breeding and breeding life history stages.

The timing of life history stages and population-level synchrony

Typically, the term seasonality implies a synchronous, periodic trend in one or more variables. Populations of birds around the world rarely exhibit strong asynchrony in reproduction (Stutchbury & Morton 2001), but there are some conditions which select for this, including

nesting habitat limitation and consistent availability of resources permitting successful reproduction year-round (Stonehouse 1962; Snow 1965; Ashmole 1968). Seasonal synchrony of reproductive behavior has been documented in previous studies of tropical *Z. capensis* populations (e.g., Miller 1959, Miller & Miller 1968; Wolf 1969; Kalma 1970; King 1973; Moore et al. 2005) and in the majority of temperate and tropical bird species that have been studied (Stutchbury & Morton 2001). Nevertheless, in previous studies of seasonally reproducing tropical *Z. capensis*, some individuals appear to be able to breed successfully though they are out-of-synch with the rest of the population (Miller & Miller 1968; Wolf 1969; Kalma 1970). In our study population we observed every life history stage in every sampling period without any apparent trend toward seasonal breeding (Fig. 2.2). Our results suggest individual pairs of *Z. capensis* are on behavioral schedules that do not necessarily correlate with the schedules of other pairs in the population. Similarly, several studies of equatorial seabird populations show asynchronous breeding schedules, potentially owing to fierce competition for limited nest-sites and the year-round abundance of several sources of fish prey (Stonehouse 1962; Snow 1965; Ashmole 1968; Harris 1969).

In environments with extremely low variability in temperature, high rainfall year-round and little change in photoperiod throughout the year, such as the focal population, life cycles of individual pairs can easily become asynchronously timed within a population. Cycles of life history stages are hypothesized to occur according to internal condition and circumstance if there is a lack of strong or meaningful environmental cues (Stonehouse 1962; Ashmole 1968; Harris 1969). Populations such as the focal population and colonies of tropical seabirds are producing young year-round and these birds must wait to find territory spaces and to begin reproductive cycles, leading to asynchrony in the initiation of life cycles within the population (Smith 1978). Moreover, if the nest of one pair fails during incubation and the pair begins to molt, but in another pair reproduction continues successfully until young reach independence before molt starts, those two pairs could be months apart in terms of the timing of life history stages (Ashmole 1968). In populations exhibiting strong asynchrony of life history stages due to the lack of strong and/or meaningful environmental cues, pairs of birds are considered to use social cues to synchronize their life cycles (Ashmole 1968). In the study population the life history stage of a given pair does not appear to correspond to large-scale seasonality in the environment,

but may depend on to external circumstance (e.g., is reproduction successful), internal condition, and social cues.

Conclusions

Similar to temperate breeding *Zonotrichia*, high aggression responses are observed during pre-breeding in individual *Z. capensis* in Las Caucheras, suggesting the paternity defense is a selective force acting in the study population. However, unlike temperate-zone birds that defend breeding territories, territorial aggression responses do not decline as individuals move from pre-breeding to nesting, when territorial responses and male hormones controlling aggression have been shown to interfere with paternal care (Wingfield & Moore 1987). Thus, there may be different hormone-behavior relationships in Las Caucheras *Z. capensis*. Lower levels of defense during the feeding fledglings, molting and non-breeding life history stages suggests that year-round defense of territorial space to attract and/or keep mates also appears to be essential in this tropical population. This is similar to year-round territorial temperate species that may reduce defense or territory size, but still defend territory spaces at some level to secure nesting sites for the subsequent season. Therefore, in the focal population, multiple factors appear to be influencing the evolution of territorial aggression, with peak aggression being most associated with life history stage and not with a specific time of the year.

The population-level asynchrony of individual life history stages in Las Caucheras is distinct from the majority of temperate latitude territorial birds, where breeding territoriality occurs in a specific temporal period of the year. Tropical environments tend to have less pronounced and/ or less predictable seasonal temperature and rainfall cycles than temperate-zone environments (Stutchbury & Morton 2001). This implies that factors influencing the timing of reproduction and associated territorial behavior in the focal population are not related to environmental seasons *per se*. Rather, factors influencing the timing of behaviors are likely to vary on the scale of individual reproductive histories and stochastic events affecting life cycle timing. This timing regime has also been observed in tropical seabirds and suggests that limits on timing are mainly internal in situations where large-scale environmental cues are absent or meaningless to the breeding cycle of the population in question (Stonehouse 1962; Snow 1965).

Acknowledgements

We thank los Flacos and la familia Luís for permitting us to use their land. We appreciate the cooperation of many farmers in working around mist nets and helping with livestock maneuvering. Thanks to J.F. Husak and P. Widder, who gave advice and critique of figures and statistical analyses. We also acknowledge H. Wada, A. Kumar, C. Eikenaar, J.R. Moore who provided suggestions regarding early drafts of this manuscript. Special thanks to J.R. Walters and B.G. Freeman who gave valuable critique that greatly improved later versions of this manuscript. We also thank T.W. Small for help with Ecuadorian logistics, and moral support and P. Martin and S. Lynn for help in making intruder mounts. Funding was provided from the National Science Foundation (IOS 0545735). The research described above adhered to animal care protocols by the IUCAC of Virginia Tech and Ecuadorian regulations.

Literature Cited

- Ashmole, N. P. 1968 Breeding and molt in the white tern (*Gygis alba*) on Christmas Island, Pacific Ocean. *The Condor* **70**, 35-55.
- Baker, J. R. 1938 The relation between latitude and breeding seasons in birds. *Proc. Zool. Soc. London* **108**, 557-582.
- Bendix, J. & Rafiqpoor, M. D. 2001 Studies on the thermal conditions of soils at the upper tree line in the páramo of Papallacta (eastern cordillera of Ecuador). *Erdkunde* **55**, 257-276.
- Bronson, F. H., Heideman, P. D. 1992 Lack of reproductive photoresponsiveness and correlative failure to respond to melatonin in a tropical rodent, the cane mouse. *Biology of Reproduction* **46**:246-250
- Brown, J. L. 1964 The evolution of diversity in avian territorial systems. *The Wilson Bulletin* **76**, 160-169.
- Brown, G. P. & Shine, R. 2002 Reproductive ecology of a tropical natricine snake, *Tropidonophis mairii* (Colubridae). *Journal of Zoology* **258**, 63-72.
- Busch, D. S., Wingfield, J. C. & Moore, I. T. 2004 Territorial aggression of a tropical passerine, *Zonotrichia capensis*, in response to a variety of conspecific intruders. *Behaviour* **141**, 1173-1188.

- Chandola-Saklani, A., Thapliyal, A., Negi, K., Diyundi, S. C. & Choudhary, B. 2004 Daily increments of light hours near vernal equinox synchronize circannual testicular cycle of tropical spotted munia. *Chronobiology International* **21**, 553-569.
- Crook, J. H. 1960 Studies on the reproductive behavior of the Baya weaver (*Ploceus philippinus* (L)). *Journal of the Bombay Natural Historical Society* **57**, 1-44.
- Crook, J. H. 1963 The Asian weaver birds; problems of coexistence and evolution with special reference to behavior. *Journal of the Bombay Natural Historical Society* **60**, 1-48.
- Crook, J. H. 1964 The Evolution of Social Organisation and Visual Communication in the Weaver Birds (*Ploceinae*). In *Behavior Supplement*, vol. 10, pp. 1-187.
- Cumming, G. S. & Bernard, R. T. F. 1997 Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**, 309-317.
- Davis, J. 1971 Breeding and molt schedules of the rufous-collared sparrow in coastal Peru. *The Condor* **73**, 127-146.
- Dawson, A. 2006 Control of molt in birds: Association with prolactin and gonadal regression in starlings. *General and Comparative Endocrinology* **147**, 314-322.
- Dinerstein, E. 1986 Reproductive Ecology of Fruit Bats and the Seasonality of Fruit Production in a Costa Rican Cloud Forest. *Biotropica* **18**, 307-318.
- Dunn, A. M., Copelston, M. & Workman, L. 2004 Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis* **146**, 77-84.
- Dunn, A. M. & Zann, R. A. 1996 Undirected song in wild zebra finch flocks: Contexts and effects of mate removal. *Ethology* **102**, 529-539.
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002 Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**, 2195-2212.
- Harris, M. P. 1969 Factors influencing the breeding cycle of the red-billed tropicbird in the Galapagos Islands. *Ardea* **57**, 149-157.
- Hartmann, M. T., Del Grande, M. L., da Costa Gondim, M. J., Mendes, M. C. & Marques, O. A. V. 2002 Reproduction and activity of the snail-eating snake *Dipsas albifrons* (*Colubridae*) in the southern Atlantic forest in Brazil. *Studies on Neotropical Fauna and Environment* **37**, 111-114.
- Hau, M., Perfito, N. & Moore, I. T. 2008 Timing of breeding in tropical birds: Mechanisms and evolutionary implications. *Ornitologia Neotropical* **19** (Suppl.), 39-59.

- Hau, M., Wikelski, M., Gwinner, H. & Gwinner, E. 2004 Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* **106**, 489-500.
- Hau, M., Wikelski, M. & Wingfield, J. C. 1998 A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 89-95.
- Hockey, P. A. R. & Wilson, W. A. 2003 Reproductive traits of marine terns (*Sternidae*): evidence for food limitation in the tropics? *Ostrich* **74**, 110-116.
- Jacobs, J. D. & Wingfield, J. C. 2000 Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* **102**, 35-51.
- Kalma, D. L. 1970 Some aspects of the breeding ecology and annual cycle of three populations of the rufous-collared sparrow (*Zonotrichia capensis*) in Western Panama. Ph.D. dissertation, Yale University.
- King, J. R. 1973 The annual cycle of the rufous-collared sparrow (*Zonotrichia capensis*) in three biotopes in northwestern Argentina. *Journal of Zoology, London* **170**, 163-188.
- Kokko, H. 1999 Cuckoldry and the stability of biparental care. *Ecology Letters* **2**, 247-255.
- Kokko, H., Gunnarsson, T. G., Morrell, L. J. & Gill, J. A. 2006 Why do female migratory birds arrive later than males? *Journal of Animal Ecology* **75**, 1293-1303.
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W. C. 2001 Pseudoreplication in playback experiments, revised a decade later. *Animal Behavior* **61**, 1029-1033.
- Marler, C. A. & Moore, M. C. 1988 Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology and Sociobiology* **23**, 21-26.
- Miller, A. H. 1959 Reproductive cycles in an equatorial sparrow. *Proceedings of the National Academy of Sciences* **45**, 1095-1100.
- Miller, A. H. 1962 Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences* **48**, 396-400.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, M. C. & Marler, C. A. 1987 Effects of testosterone manipulations on nonbreeding season territorial aggression in free-living male lizards, *Sceloporus jarrovi*. *General and Comparative Endocrinology* **65**, 225-232.

- Moore, I. T., Perfito N., Wada H., Sperry T. S., Wingfield J. C. 2002 Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. *General and Comparative Endocrinology* **129**, 13-19.
- Moore, I. T., Wada, H., Perfito, N., Busch, D. S. & Wingfield J. C. 2004a Territoriality and testosterone in an equatorial population of rufous-collared sparrows, *Zonotrichia capensis*. *Animal Behaviour* **67**, 411-420.
- Moore, I. T., Walker, B. G. & Wingfield, J. C. 2004b The effects of combined aromatase inhibitor and antiandrogen on male territorial aggression in a tropical population of rufous-collared sparrows, *Zonotrichia capensis*. *General and Comparative Endocrinology* **135**, 223-229.
- Moore, I. T., Bonier, F. & Wingfield, J. C. 2005 Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology* **16**, 755-762.
- Murphy, M. E. 1996 Energetics and nutrition of molt. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 158-198. New York: Chapman and Hall.
- Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford, U. K.: Clarendon Press.
- O'Brian, G. M. 1993 Seasonal reproduction in flying foxes, reviewed in context of other tropical mammals. *Reproduction, Fertility and Development* **5**, 499-521.
- Perfito, N., Kwong, J. M. Y., Bentley, G. E. & Hau, M. 2008 Cue hierarchies and testicular development: Is food a more potent stimulus than day length in an opportunistic breeder (*Taeniopygia g. guttata*)? *Hormones and Behavior* **53**, 567-572.
- Ricklefs, R. 1966 The temporal component of diversity among species of birds. *Evolution* **20**, 235-242.
- Saint-Girons, H. 1982 Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* **38**, 5-16.
- Scheuerlein, A. & Gwinner, E. 2002 Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. *Journal of Biological Rhythms* **17**, 171-180.
- Schieltz, P. C. & Murphy, M. E. 1997 The contribution of insulation changes to the energy cost of avian molt. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **75**, 396-400.

- Scriba, M. & Goymann, W. 2008 The decoy matters! Hormonal and behavioural differences in the reaction of territorial European robins towards stuffed and live decoys. *General and Comparative Endocrinology* **155**, 511–516.
- Shine, R. & Brown, G. P. 2008 Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 363-373.
- Sinclair, A. R. E. 1978 Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants in a tropical African savannah. *Ibis* **120**,480-497.
- Skutch, A. F. 1950 The nesting seasons of Central American birds in relation to climate and food supply. *Ibis* **92**, 185-222.
- Smith, S. M. 1978 The “underworld” in a territorial sparrow: Adaptive strategies for floaters. *American Naturalist* **112**, 571-582.
- Snow, D. W. 1965 The breeding of the red-billed tropic bird in the Galapagos Islands. *The Condor* **67**, 210-214.
- Stonehouse, B. 1962 The tropicbirds (genus *Phaethon*) of Ascension Island. *Ibis* **103B**, 124-161.
- Stutchbury, B. J. M & Morton, E. S. 2001 *Behavioral ecology of tropical birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993 The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics* **24**, 353-377.
- Weatherhead, P. J. & Yezerinac, S. M. 1998 Breeding synchrony and extra-pair mating in birds. *Behavioral Ecology and Sociobiology* **43**, 217-219.
- Weathers, W. W., Davidson, C. L. & Morton, M. L. 2003 Energetics of altricial nestlings in cold climates: Insights from the Mountain White-crowned Sparrow. *Condor* **105**, 707-718.
- Wikelski, M., Martin, L. B., Scheuerlein, A., Robinson, M. T., Robinson, N. D., Helm, B., Hau, M. & Gwinner, E. 2008 Avian circannual clocks: adaptive significance and possible involvement of energy turnover in their proximate control. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 411-423.

- Wingfield, J. C. & Kenagy, G. J. 1991 Natural regulation of reproductive cycles. In *Vertebrate Endocrinology: Fundamentals and Biomedical Implications*, vol. 4(ed., P. K. T. Pawg & M. P. Schreibruan). pp 181-241. San Diego: Academic Press, Inc.
- Wingfield, J. C., Lynn, S. E. & Soma, K. K. 2001 Avoiding the 'costs' of testosterone: Ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution* **57**, 239-251.
- Wingfield, J. C. & Moore, M. C. 1987 Hormonal, social, and environmental factors in the reproductive biology of free-living male birds. In *Psychobiology of Reproductive Behavior: and Evolutionary Perspective* (ed. D. Crews), pp. 149-175. New Jersey: Prentice Hall.
- Wolf, L. L. 1969 Breeding and molting periods in a Costa Rican population of the Andean sparrow. *The Condor* **71**, 212-219.

Table 2.1 Characteristics and observations used to determine five life history stages of individuals. All life history stages were checked with behavioral observation of pairs for simulated territorial intrusion experiments.

| | |
|---------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Pre-breeding | Female with defeathering or defeathered brood patch or male with cloacal protuberance ≥ 2.5 mm and observed with nest material, constructing nest, or focal territory found with freshly lined nest (no eggs laid). Captured without molting primary flight feathers. |
| Nesting | Male cloacal protuberance ≥ 5 mm length or female with edematous brood patch (for incubating eggs or nestlings), and/or known to have a clutch of eggs, or be feeding nestlings, and not molting primary flight feathers. |
| Feeding fledglings | Observed feeding and following fledglings in or around defined territory and were not molting primary flight feathers. |
| Molting | Caught with 1 or more primaries molting prior to experiment, recaptured with progressed molt or having completed molt post-experiment; male with cloacal protuberance ≤ 1 mm length; female without brood patch. Focal pair was not constructing a nest, incubating, nor feeding young. |
| Non-breeding | Male cloacal protuberance ≤ 1 mm length or female without brood patch and two or more of the following observations: not building a nest or incubating, not feeding fledglings, not molting any primary flight feathers. |

Table 2.2 Principal component 1 (PC1) loadings for behavioral responses to simulated territorial intrusions in five different life history stages.

| | PC1 loadings |
|----------------------------|--------------|
| Time within 5 | 0.50 |
| Closest approach (m) | -0.51 |
| Number of songs | 0.50 |
| Number of song-switches | 0.37 |
| Number of flights | 0.31 |
| Eigenvalue | 2.7337 |
| Percent variance explained | 54.7 |

Principal component analysis was used to determine a single composite behavioral response variable, the ‘aggression score’, for each male. Mean aggression scores in each treatment group (pre-breeding, nesting, feeding fledglings, molting, non-breeding) were then compared.

Table 2.3 Aggressive behaviors divided among simulated territorial intrusion periods (pre-STI, STI, post-STI) and among life history stages. Means \pm standard error are given for all behaviors used to compile PC1 scores for individual males. Each behavioral response is compared within a given STI period, as well as among life history stages (life history stages; e.g., nesting, molting). Note that the latency of response to the intrusion was only recorded in the STI period and persistence of response was only recorded in the post-STI period, thus these were not included in PC1 scores. One-way ANOVAs were used to test for significant differences in measured behaviors among different life history stages. If there were significant differences, Tukey-Kramer post-hoc tests were used to determine where differences existed among life history stages for each behavior. Distinct superscript letters denote significant differences in responses among life history stages, but within STI periods (e.g., did birds in the nesting life history stage sing more frequently in response to a decoy than birds tested in pre-breeding, feeding fledglings molting or non-breeding life history stages within the STI period of the experiment).

| Life history stage | | Pre-breeding | | | Nesting | | | Feeding fledglings | | | Molting | | | Non-breeding | | |
|--------------------|-------------------------|--------------------------------|--------------------------------|--------------------------------|---------------------------------------------|--------------------------------|---------------------------------------------|--------------------------------|---------------------------------------------|--------------------------------|---------------------------------------------|--------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|
| STI period | pre-STI | STI | post-STI | pre-STI | STI | post-STI | pre-STI | STI | post-STI | pre-STI | STI | post-STI | pre-STI | STI | post-STI | |
| Measured Behaviors | time within 5 m | 6.84 ± 0.82 ^a | 9.48 ± 0.60 ^a | 8.99 ± 0.77 ^a | 5.12 ± 0.66 ^a _b | 8.73 ± 0.48 ^a | 7.38 ± 0.67 ^a _b | 1.73 ± 0.85 ^c | 5.84 ± 0.62 ^b _c | 3.87 ± 0.79 ^c | 1.61 ± 0.85 ^c | 4.33 ± 0.62 ^c | 2.88 ± 0.79 ^c | 2.56 ± 0.78 ^b _c | 7.19 ± 0.57 ^a _b | 5.29 ± 0.72 ^b _c |
| | closest approach (m) | 3.38 ± 0.49 ^a | 1.03 ± 0.30 ^a | 1.09 ± 0.41 ^a | 3.00 ± 0.39 ^a | 1.12 ± 0.24 ^a | 1.84 ± 0.33 ^a | 6.67 ± 0.51 ^b | 2.20 ± 0.31 ^a _b | 4.13 ± 0.42 ^b | 5.80 ± 0.51 ^b | 2.81 ± 0.31 ^b | 4.47 ± 0.42 ^b | 6.00 ± 0.46 ^b | 2.31 ± 0.28 ^b | 3.92 ± 0.38 ^b |
| | number of songs | 9.38 ± 1.46 ^a | 32.3 ± 2.98 ^a | 25.5 ± 2.56 ^a | 6.96 ± 1.17 ^a | 31.1 ± 2.39 ^a | 19.3 ± 2.05 ^a | 0.20 ± 1.51 ^b | 5.53 ± 3.08 ^b _c | 1.13 ± 2.64 ^b | 0.00 ± 1.51 ^b | 4.00 ± 3.08 ^c | 3.07 ± 2.64 ^b | 0.50 ± 1.38 ^b | 17.1 ± 2.81 ^b | 6.78 ± 2.41 ^b |
| | number of song-switches | 0.06 ± 0.05 ^a | 0.94 ± 0.42 ^a | 1.13 ± 0.21 ^a | 0.08 ± 0.04 ^a | 0.64 ± 0.17 ^a | 0.07 ± 0.22 ^a _b | 1.84 ± 0.33 ^a | 0.40 ± 0.44 ^a | 0.07 ± 0.17 ^b | 0.00 ± 0.05 ^a | 0.13 ± 0.44 ^a | 0.20 ± 0.22 ^b | 0.00 ± 0.04 ^a | 1.11 ± 0.40 ^a | 0.39 ± 0.20 ^a _b |
| | number of flights | 6.84 ± 0.82 ^a | 7.50 ± 1.54 ^a | 4.19 ± 0.66 ^a | 2.24 ± 0.24 ^a | 5.48 ± 1.24 ^a | 2.92 ± 0.53 ^a | 1.84 ± 0.33 ^a | 4.73 ± 1.59 ^a | 1.47 ± 0.69 ^b | 1.27 ± 0.31 ^a _b | 5.73 ± 1.59 ^a | 2.00 ± 0.69 ^a _b | 1.06 ± 0.28 ^b | 6.78 ± 1.46 ^a | 1.56 ± 0.63 ^b |
| | latency | < | 0.59 ± 0.52 ^a | < | < | 0.89 ± 0.42 ^a | < | < | 2.50 ± 0.54 ^a _b | < | < | 3.84 ± 0.54 ^b | < | < | 2.20 ± 0.49 ^a _b | < |
| | persistence | < | < | 8.66 ± 0.78 ^a | < | < | 6.98 ± 0.63 ^a _b | < | < | 3.64 ± 0.81 ^c | < | < | 2.91 ± 0.81 ^c | < | < | 5.27 ± 0.74 ^b _c |

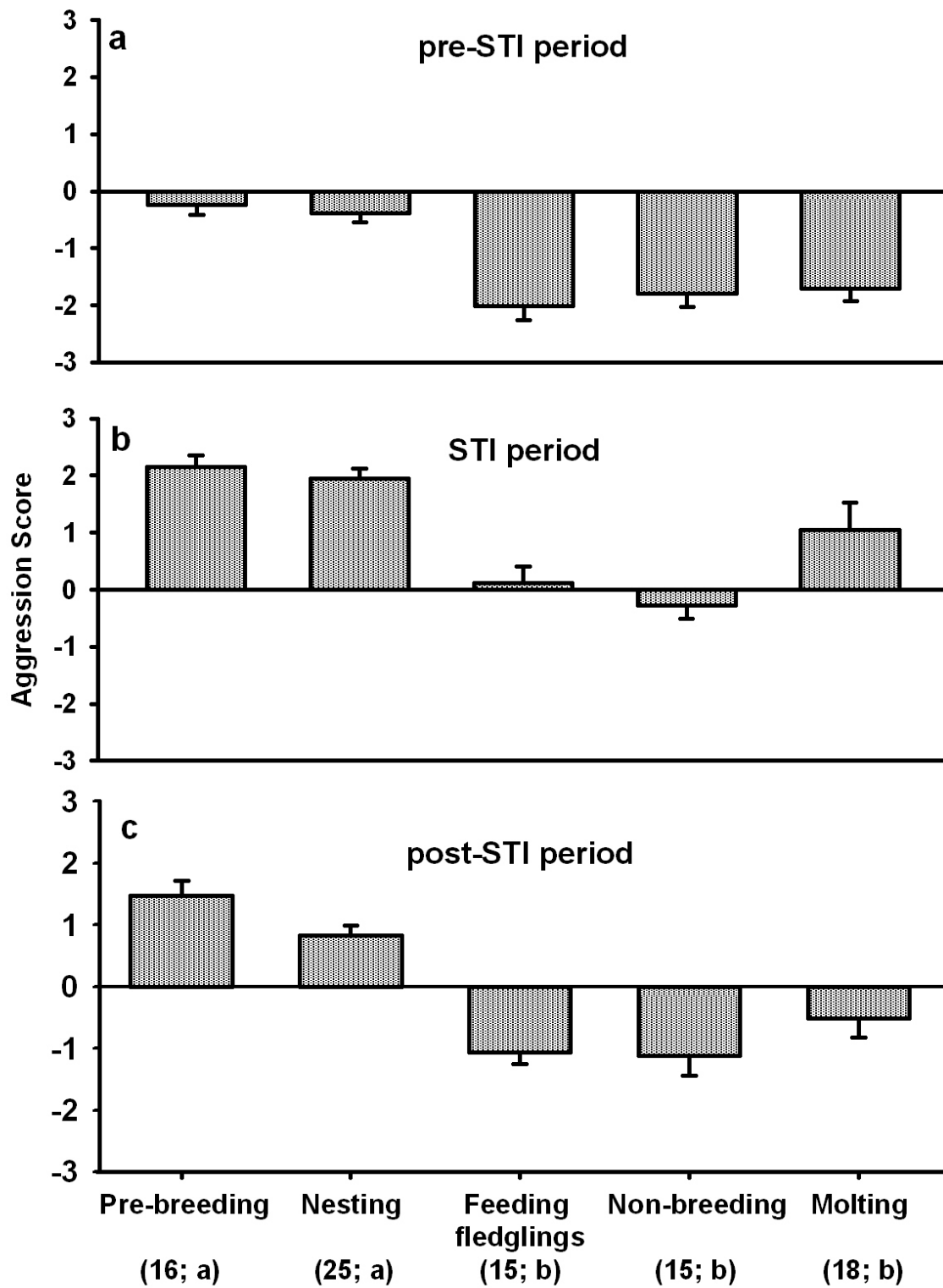


Figure 2.1 Mean aggression scores (\pm SE) among males in five life history stages. Males in each life history stage: pre-breeding, nesting, feeding fledglings, molting, non-breeding were tested across three simulated territorial intrusion (STI) periods (a: Pre-STI, b: STI, c: Post-STI). Repeated measures two-way ANOVA followed by Tukey-Kramer HSD post-hoc analysis revealed significant differences among STI periods (a, b, c; $p < 0.0001$). Numbers in parentheses are sample sizes, followed by letters showing significant differences among life history stages when the letters are different. See text for statistical difference values.

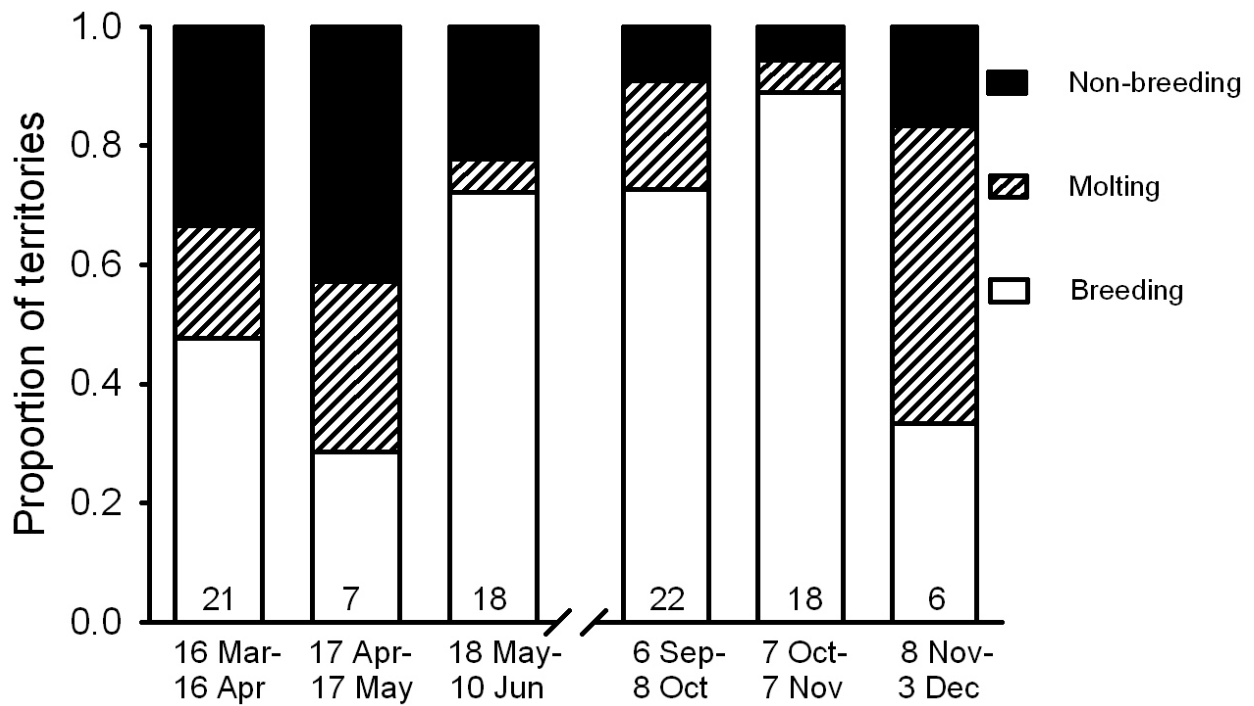


Figure 2.2 The proportion of territories in each life history stage during two periods (March - June and September - December 2007). Note that at any given time, some proportion of pairs were found in each life history stage within the population. Pre-breeding, nesting and feeding-fledglings life history stages were combined into a single breeding category for clarity. Sample sizes for total number of territories identified during each sampling period are at the bottom of bars. Note that three territories identified during the sampling periods, but not included in the simulated territorial intrusion analysis, are included here because their life history stages were known.

CHAPTER III. IS THERE A TRADE-OFF BETWEEN CARING FOR OFFSPRING AND TERRITORIAL AGGRESSION IN TROPICAL MALE RUFIOUS-COLLARED SPARROWS (*ZONOTRICHIA CAPENSIS*)?

Alexandra M. Class and Ignacio T. Moore

Abstract

Biparental care is more common in birds than in any other vertebrate class. In those bird species exhibiting biparental care, the degree of parental care provided by each sex depends on sex-specific fitness costs and benefits. As males typically invest less initially into reproduction, they are more likely to trade-off time and energy that might later be invested into paternal care for alternative activities, such as searching for extra-pair mating opportunities. The trade-off between paternal care and territorial aggression is particularly important because of associated benefits (e.g. high paternal provisioning can increase offspring fitness, aggressive defense of mates can increase paternity) and costs (e.g. increased adult predation risk, loss of paternity). Such trade-offs have been relatively well studied in temperate species compared to tropical species. Unlike temperate-zone breeding bird species, many tropical birds exhibit a syndrome of a 'slow pace of life' characterized by delayed maturation, low fecundity and high survival. Thus, it is reasonable to expect that tropical birds may experience different trade-offs relative to temperate species. Some characteristics of the tropical slow pace of life (smaller clutch size and slower development) may be associated with decreased paternal provisioning. We studied an equatorial population of rufous-collared sparrows (*Zonotrichia capensis*) to investigate trade-offs between paternal care and aggression in a system in which biparental care occurs and clutch size is typically two eggs. We found no direct trade-off between vigilance or aggression and paternal provisioning rate. However, nestling body size was positively related to male provisioning rate and negatively related to female provisioning rate. Our data suggest a time/energy trade-off between male and female care, but not between male aggression and paternal care.

Introduction

Biparental care is more common in birds than in any other vertebrate class (Ar & Yom-Tov 1978; Silver et al. 1985; Clutton-Brock 1991). Among bird species, biparental care is particularly common among socially monogamous birds (Lack 1968; Silver et al. 1985; Clutton-Brock 1991). In socially monogamous birds exhibiting biparental care, theory predicts that the sexes will be in conflict because of sex-specific fitness benefits and costs of providing care (Trivers 1974; Smith 1977; Parker & Schwagmeyer 2005). Thus, females must weigh the benefits of providing care to their offspring against their own self-maintenance and potential future reproduction (e.g., current care may be to the detriment of future fecundity and/or survival) (Smith 1977). Males also face the decision of trading time and energy invested in providing for their offspring (potentially increasing offspring survival and the probability that they reproduce) for time and energy invested in self-maintenance towards increasing their own survival probability (Trivers 1974; Smith 1977). Males typically invest less initially into reproduction (Trivers 1972, 1974; Smith 1977). Therefore, males could stand to gain more in terms of fecundity by trading investment in current reproduction for alternative activities, including territorial aggression (Wingfield et al. 1990; Ketterson et al. 1992; Pryke & Griffith 2009) and searching out copulations with females other than their social mate (Trivers 1974; Smith 1977; Kokko 1999; Kokko & Morrell 2005). Aggressive defense of the territory is a major time and energy investment for males that typically overlaps with reproductive periods during which paternal care may be critical (Sargent & Gross 1985; Wingfield et al. 1990; Ketterson et al. 1992).

Aggressive territorial defense can be beneficial in that males can defend their paternity (defend against other males searching for extra pair copulations), as well as their mates and young from threats, including predators and intruders (Hegner & Wingfield 1987; Wingfield et al. 1990; Ketterson et al. 1992; Schoech et al. 1998). However, male aggression during the reproductive period can have negative consequences (Marler & Moore 1988; Wingfield 1990). For instance, misplaced male aggression could harm offspring (Wingfield & Moore 1987; Wingfield et al. 1990). More aggressive males may also experience fitness costs, such as increased predation risk (Marler & Moore 1988). Further, antagonistic behavior requires considerable time and energy that could be spent providing for offspring (Wingfield et al. 1990; Wolf et al. 1990; Ketterson & Nolan 1994), potentially resulting in a decrease in nestling size at

fledging (e.g., Ricklefs & Starck 1998; Lynn et al. 2009; Pryke & Griffith 2009) and/or offspring survival (e.g., Wolf et al. 1988, 1991; Pryke & Griffith 2009). In most socially monogamous bird species with biparental care, male aggression declines from early breeding (when defense of territories and competition for mates is high) to later breeding, when males may gain more by providing for their offspring in terms of higher offspring growth and survival (for review see Wingfield 1990; Ketterson & Nolan 1994; Wingfield 2000; Wingfield et al. 2000). Male territorial aggression is often mediated by the steroid hormone testosterone (Wingfield & Moore 1987; Wingfield et al. 1990). In socially monogamous birds testosterone typically declines in parallel with the need for paternal care because testosterone is also known to inhibit paternal care in many species (for a review see Wingfield et al. 1987; Wingfield et al. 1990; Atkins-Regan 2005). Nevertheless, males have the physiological ability to respond to threats by temporarily mounting an aggression response during the paternal care phase (Wingfield et al. 1990; Atkins-Regan 2005). Trade-offs between aggression and paternal care (often mediated by testosterone) are well documented, but these studies have focused primarily on seasonally breeding temperate-zone species (Hegner & Wingfield 1987; Beletsky et al. 1989; Ketterson et al. 1992; Schoech et al. 1998; Clotfelter et al. 2007, but see Lynn et al. 2009).

Biparental care is common among species breeding in seasonal environments such as the temperate-zone (i.e., the region above the Tropic of Cancer and below the Tropic of Capricorn, 23° 26'N and S, respectively). In the temperate-zone breeding is temporally constrained to when resources are abundant and the climate is benign (see for review Lofts & Murton 1968; Wingfield et al. 2000). Seasonal peaks in food availability select for faster nestling growth (Bortolotti 1989; Ricklefs & Starck 1998), faster foraging, and increased provisioning rate (Newton 1972). Thus, temperate-zone breeding bird species take advantage of long day length and highly abundant resources to provide for large broods and/or multiple broods in their breeding season (Charnov & Krebs 1974; Klomp 1970; Martin et al. 2000a; Jetz et al. 2008). Biparental care, in which males as well as females contribute to provisioning young, may therefore be selectively advantageous because of temporal and energetic demands on adults to adequately care for larger broods in a shorter amount of time (Trivers 1972; Clutton-Brock 1991).

The vast majority of bird species breed in the tropics (~80% of all passerines, Stutchbury & Morton 2001). Tropical bird species exhibit a great diversity in life history characteristics,

territorial systems and behavior (Martin 1996, 2004; Stutchbury & Morton 2001). Despite this diversity, most tropical birds studied to date are socially monogamous and exhibit biparental care (Stutchbury & Morton 2001, 2008). In contrast to the seasonal peak in food availability, which characterizes temperate-zone environments, there is typically less predictability in year-to-year timing of seasons and in the amplitude of seasonal change in the tropics (Janzen 1973; Hails 1982). Thus, selection has favored smaller broods (Buckley et al. 1985; Jetz et al. 2008), slower nestling growth rates (Ricklefs 1969; Ricklefs & Starck 1998) and often one brood per breeding period in many tropical bird species. Nevertheless, most generalizations about tropical birds are based on a small number of studies. To our knowledge, there have not been studies on the trade-offs between paternal care and territorial aggression in wild tropical birds (but for a study of a captive-bred tropical species see Pryke & Griffith 2009).

The genus *Zonotrichia* is well studied compared to most wild bird species (e.g. Chapman 1940; Blanchard 1941; Miller & Miller 1968; Davis 1971; Morton 2002). The rufous-collared sparrow, *Zonotrichia capensis*, is the single tropical species of the five species within the *Zonotrichia* genus. The range of *Z. capensis* extends from southern Chiapas, Mexico to Tierra del Fuego, Argentina and altitudes from sea level to 5300 m. In the twenty *Z. capensis* subspecies currently recognized, there is considerable diversity in life history characteristics, seasonality of reproduction and diet (Chapman 1940; Miller & Miller 1968; Kalma 1970; Davis 1971; King 1973; Castro et al. 1985; Fotheringham 1995; Ruiz et al. 1995). Unlike many other tropical species, it is both numerous and easy to observe, partly because it adapts readily to agricultural and environmental alteration (Miller & Miller 1968). Across their range *Z. capensis* are socially monogamous and exhibit biparental care, but the degree of care is highly variable (e.g., Kalma 1970; Miller & Miller 1968). Tropical species, including *Z. capensis*, have slower nestling growth and developmental rates than temperate-zone or arctic species (tropical *Z. capensis* nestling period: ~12 days, Miller & Miller 1968; temperate *Z. leucophrys* nestling period: ~9-10 days, Morton 2002). Nevertheless, the 12-day nestling period is a period of rapid growth and development similar to that described for temperate *Zonotrichia* (Morton 2002). In both temperate *Zonotrichia* and tropical *Z. capensis* this period is marked by substantial increase in body mass, alertness, coordinated movements, feather growth and thermoregulatory ability (Morton 2002). The percentage of extra pair paternity of *Z. capensis* in Papallacta, Ecuador, is also considered to be comparable to temperate-zone congeners (~50%, Bonier unpub. data).

Thus, investigations of *Z. capensis* can add to our knowledge of tropical systems in general, while remaining within a well-studied genus, limiting phylogenetic confounds that hinder comparisons among tropical and non-tropical species (Zink & Blackwell 1996; Moore et al. 2002).

We studied the trade-off of paternal care and aggression in tropical *Z. capensis* because previous studies have shown fundamentally different hormone-behavior relationships than temperate congeners. Previous studies show that *Z. capensis* does not respond to simulated territorial intrusions, used to elicit aggressive responses from territorial males, by increasing androgen (male sex steroid hormone) production and release in either the pre-breeding or nesting periods (Moore et al. 2004a). Aggression responses also did not differ among control and experimental male birds given an androgen inhibitor and anti-estrogen (Moore et al. 2004b). Thus, contrary to the majority of previous studies of birds, males continued to display aggressive behavior during the breeding season regardless of androgen levels (Moore et al. 2004a, b). However, elevated exogenous testosterone (an androgen hormone) was associated with decreased paternal care in males within the same population (Lynn et al. 2009). Androgens may therefore influence the ability of males to provide care, as has been commonly found in male birds breeding in the temperate-zone (Wingfield & Moore 1987; Wingfield et al. 1990). These studies paint a unique picture of the proximate hormone-behavior relationship in equatorial *Z. capensis* and suggest that a hormone(s) other than testosterone may be responsible for male territorial behavior, which could influence ultimate trade-offs of territorial behavior and paternal care in *Z. capensis* (and other tropical bird species). We hypothesized that we would find no correlation between the ultimate trade-off of male territorial aggression scores and paternal provisioning rate in tropical *Z. capensis*. We predicted that male provisioning rate would not depend on male territorial aggression scores.

Methods

Focal site, population and monitoring

The focal population is located in the eastern Andes of Ecuador in the rural township of Las Caucheras, Napo Province (0°36'S, 77°54'W; altitude ~2100 m). In this population *Z. capensis* inhabit natural gaps in intact cloud forest, young second-growth forest and grazing pastures. Monthly accumulated rainfall is between 130 - 240 mm from October to March and 280 - 390

mm from April to September, though there is consistent high rainfall over the course of the year (~2500 - 3500 mm, Instituto Nacional de Meteorológica, Ecuador). Mean monthly air temperature remains nearly constant in this location (~17° C, Instituto Nacional de Meteorológica, Ecuador). In Las Caucheras daily photoperiod varies minimally over the course of the year because the site is equatorial.

We monitored territorial pairs of *Z. capensis* from 6 September – 3 December, 2007. Throughout the population, we passively captured individuals with mist nets on a daily basis for identification and monitoring. All new captures received a unique combination of color bands and a numbered aluminum band. In addition to daily passive mist-netting, we actively targeted specific territorial residents to band previously unknown individuals. We took morphological measurements of every captured bird (i.e., mass, wing length, tarsus, fat, reproductive morphology and molt).

Defining territories and nestling age classes

Since this study focused on nesting pairs, we searched for nests for at least one hour per day, when daily activities and the weather permitted. We also conducted daily observations of birds to identify monogamous pairs and their territories. Territories were designated as we found nests and pairs associated with each nest. The vast majority of nests found contained two nestlings (n = 21, total nests = 24), the median clutch size for tropical *Z. capensis* (Miller & Miller 1968). We did not include nests with different clutch sizes (i.e., 1 or 3 nestlings) in our experiments to avoid an effect of clutch size on provisioning rate.

Similar to other investigations of *Zonotrichia* (Morton & Carey 1971; Wada et al. 2007), we divided the nestling time period into three age classes (described in days based on different growth and developmental stages: age class 1, 1-3 days; age class 2, 4-8 days; and age class 3, 9-12 days (see Table 3.1). We categorized the nestlings by these three age classes to test if provisioning and male aggression varied with nestling age class. We determined nestling age by hatching date. In the case that we found a nest with very young nestlings, we used previously described nestling age descriptions, as well as our own notes on nestling size and characteristics at specific ages, to determine nestling age (Miller & Miller 1968; Morton & Carey 1971; King & Hubbard 1981).

Provisioning observations

We observed each nest three times, once during each of the nestling age classes. Each observation period lasted one hour, during which we monitored and recorded provisioning rates of both male and female adults using binoculars, a spotting scope, and/or a video camera. We sat in a hidden location at least 20 meters from the nest to minimize effects of the researcher on adult behavior and to avoid attracting potential predators. We measured nestling mass and tarsus when nestlings were approximately 8 days old (i.e., when nestlings had just finished their largest growth period, see above description) using a Pesola spring scale and calipers, respectively. We performed a linear regression of individual nestling mass (g) on tarsus (mm). We used the residuals from this regression as a body size index for individual nestlings (Constantini et al. 2009). The body size index was used later in regressions with other behavioral measures.

Simulated territorial intrusion protocol

We conducted three simulated territorial intrusion experiments (STIs) on each male (one during each nestling age class) to compare aggression responses of territorial males in each period. While both live and stuffed decoy types have been used in STI experiments, a recent study suggested that stuffed decoys can illicit stronger aggression responses (Scriba & Goymann 2008) and in initial STI trials we observed no difference in male responses to live or stuffed decoys. Therefore, we used three stuffed decoys from the study population, mounted on a stick, for all STIs. We defined central areas in each territory by observing the frequency of use of specific landmarks (such as bushes, logs, and trees) by focal males while they were singing, foraging and perching. Landmarks and areas most frequently occupied were used as guide-points to approximate territory boundaries and central areas, in which we placed the decoy and playback equipment for STIs. One day prior to each STI we paced out a 5 m radius around the territory center to insure more accurate estimates of distance and time. Immediately prior to each experiment, we placed the decoy and song playback equipment in the defined territory center, after focal males were located visually. During the STIs, we stood at least 20 m from the territory center, at which distance we were presumably not perceived as a threat (i.e., no chipping/flights directed at the observer in a trial period at least 24 hrs prior to the experiment).

Each STI consisted of three consecutive 10 min observation periods. In the first 10 min of the observation period (0 - 10 min), the decoy was covered and there was no song playback. This

period determined background territorial activity levels (hereafter referred to as the vigilance period) and thus served as a control. After this initial period, we uncovered the decoy and started a song playback track that ran for the next 10 min period (10 - 20 min) of observation (hereafter the aggression period). This period was used to measure the territorial aggression response. For each STI we selected a single song for playback from 12 song tracks recorded from 12 different males in 2006. None of the recorded males were subjects of the STI experiments described in this study. Each track had a single, randomly selected song (to avoid pseudoreplication; Kroodsma et al. 2001), followed by 9 seconds of silence, to approximate the natural song rate of *Z. capensis* in this population. Song playback and STI procedures were similar to methods used in previous studies of *Z. capensis* (Busch et al. 2004; Moore et al. 2004a). Playback volume simulated normal ranges of observed song volume, adjusted for locale. For the third 10 min observation period (20 – 30 min; hereafter the post-aggression period), we re-covered the decoy and turned off the song playback. During all three periods, we recorded the time the focal male was within 5 m of the decoy, his closest approach to the decoy (m), number of songs, number of song switches (number of times each bird used a different song type, *Z. capensis* in Las Caucheras have 2 types) and number of flights. We discuss data mainly pertaining to the vigilance and aggression periods because those periods demonstrate the difference in responsiveness of males before and after a perceived territorial threat. We attempted STIs only after territory residents were determined and when weather permitted.

Data analysis

We conducted a principal components analysis (PCA) on measured behaviors to generate a composite score corresponding to the first 10-min period (vigilance period) of the STI (hereafter referred to as the vigilance score) and for the second 10-min period of each STI (hereafter the aggression score) (Table 3.2). We used the first principal component from our PCA for all comparisons involving individual vigilance and aggression scores (Table 3.2). This methodology was used in similar studies previously (Busch et al. 2004; Moore et al. 2004a). Means of vigilance and aggression scores were compared using a repeated-measures two-way ANOVA across age classes (1, 2, and 3) and STI periods (1, 2, and 3) including interactions between age class and STI period. We used Tukey-Kramer HSD post-hoc tests to determine where there were significant differences in measured behaviors among age classes and among STI periods. We

tested correlations between vigilance and aggression scores using simple linear regressions of provisioning rates and nestling body size indices within and among different age classes.

Results

Effect of treatment and age class

There was a significant effect of the STI period on the aggression scores of males (repeated measures two-way ANOVA: $F_{2,40} = 188.86, p < 0.0001$). Post-hoc analysis revealed each STI period (the vigilance period, the aggression period, and the post-aggression period) were all significantly different from one another. The highest aggression scores occurred during the aggression period, followed by the post-aggression period and then vigilance period (Tukey-Kramer HSD; $p < 0.0001$). There was no interaction between age class and STI period (repeated measures two-way ANOVA: $F_{4,80} = 0.52, p = 0.72$).

There was a significant effect of offspring age class on aggression scores (repeated measures two-way ANOVA: $F_{2,40} = 4.28, p = 0.02$). Post-hoc analysis revealed that males had significantly lower aggression responses when they had offspring in age class 1 than in age class 2 (Tukey-Kramer HSD; $p = 0.03$). There was also a trend for males in offspring age class 1 to have lower aggression scores than males in offspring age class 3 (Tukey-Kramer HSD; $p = 0.06$). There was no difference in aggression scores between age class 2 and 3 (Tukey-Kramer HSD; $p = 0.92$).

Vigilance and provisioning rate versus aggression scores

Vigilance and aggression scores were positively, but weakly, correlated (linear regression, $r^2 = 0.21, p = 0.0002$; Fig. 3.1). There were no significant correlations between male vigilance and/or aggression scores and male provisioning rate in any age class or among age classes (Table 3.3). There was no uniform directionality in the relationship of male provisioning rate to vigilance and aggression scores (see Table 3.3 r-values). Female provisioning rates were not significantly related to male vigilance scores (Table 3.3). There was no uniform directionality in the relationship of female provisioning rate to male aggression scores (see Table 3.3 r-values).

Female versus male provisioning rate

Male provisioning rate averaged 1.03 trips per hour (males = 21; hours of observation = 63). The maximum number of male trips per hour observed was 4 (n = 1) and the minimum 0 (n = 16). Three males did not provision during any 60 min observation period. Female provisioning rate averaged 4.33 trips per hour (n = 21). The maximum female trips per hour observed was 7 (n = 1) and the minimum was 2 (n = 1). There was a significant negative relationship between female and male provisioning (linear regression, $r^2 = 0.27$ $p < 0.0001$; Fig. 3.2). As males made fewer trips per hour, females increased the number of provisioning trips per hour (Fig. 3.2). This relationship was apparent in every age class (linear regressions, offspring age class 1: $r^2 = 0.26$ $p = 0.02$; offspring age class 2: $r^2 = 0.26$ $p = 0.02$; offspring age class 3: $r^2 = 0.26$ $p = 0.02$; Fig. 3.2).

Nestling body size index and provisioning rate

Nestling mass was positively correlated with tarsus length (linear regression, $r^2 = 0.38$, $p < 0.0001$). The residuals of this relationship were used as individual nestling body size indices. Nestling body size was positively correlated with male provisioning trips per hour (linear regression, $r^2 = 0.25$ $p = 0.0008$; Fig. 3.3). However, the number of female provisioning trips per hour was negatively related to nestling body size (linear regression, $r^2 = 0.15$ $p = 0.01$; Fig. 3.3). Cumulative male and female provisioning rates did not correlate with the nestling body size index (linear regression, $r^2 = 0.00$ $p = 0.67$; Fig. 3.3). All nestlings (n = 42) of nests observed in this study survived to fledging.

Discussion

In this population of *Z. capensis* we found no direct trade-off between male vigilance or territorial aggression scores and paternal provisioning rate (Table 3.3). However, nestling body size index was positively related to male provisioning rate and negatively related to female provisioning rate (Fig. 3.3). We suggest the high variability in paternal provisioning may result from other time/energy trade-offs, which also influences female provisioning rate and nestling body size.

Life history differences can help explain why we did not find a direct relationship between paternal care and aggression in the Las Caucheras population of *Z. capensis*. Resource

availability, rate of development and growth determine how much effort and time a parent must spend caring for young. As in many tropical bird species, *Z. capensis* have smaller clutches than temperate zone or arctic breeding species (2–3 eggs/clutch vs. 4–6 eggs/clutch, respectively; Miller & Miller 1968, King & Hubbard 1981, Morton 2002, for relationship of clutch size versus latitude see Jetz et al. 2008). Tropical and temperate-zone *Zonotrichia* have fixed developmental rates (Miller & Miller 1968; King & Hubbard 1981). However, tropical species, including *Z. capensis*, develop and grow at a slower rate than temperate-zone or arctic species (tropical: Miller & Miller 1968; temperate: 9-10 days, Morton 2002). These life history characteristics fit the syndrome of a slower pace of life described for many tropical bird species and are associated with less profound seasonal peaks in food and resource availability that are characteristic of many tropical environments (Ricklefs & Wikelski 2002).

Biparental care is generally hypothesized to provide a direct fitness advantage to parents because it can lead to increased offspring survival and/or fitness (Trivers 1972; Greenlaw & Post 1985; Ricklefs & Starck 1998; Wolf et al. 1988). We observed high variability in the degree of male provisioning (some males did not provision nestlings at all, while others provisioned at an equal rate as their mate; Fig. 3.2). Female *Z. capensis* provisioned at higher rates if their mate was provisioning at a lower rate (Fig. 3.2). We interpret this relationship as females attempting to compensate for low male provisioning. However, nestlings experiencing this situation (high female provisioning paired with low male feeding) tended to have smaller body size (Fig 3.3b). Conversely, male provisioning rate was positively related to nestling size (Fig 3.3a). Thus it appears that females cannot fully compensate for poor male provisioning rates and that when males do feed the young it positively affects nestling body size. While nestling size does not necessarily predict nestling survival to fledging (Wolf et al. 1988; Ketterson et al. 1992), nestling size is often correlated with survival post-fledging: larger nestlings survive at higher rates post-fledging than smaller nestlings (Greenlaw & Post 1985; Wolf et al. 1988; Ricklefs & Starck 1998). Previous studies on Colombian *Z. capensis* found that fledgling survival was low (Miller & Miller 1968). Higher quality fledglings may also be most likely to reproduce sooner and/or have higher fecundity as a result of their larger size (Greenlaw & Post 1985; Wolf et al. 1988; Ricklefs & Starck 1998). This suggests that male provisioning rates may be important in determining fledgling survival and their future reproduction, at least in *Z. capensis* in the Las Caucheras population.

Time-energy trade-offs other than between aggression and paternal provisioning may influence the degree of paternal care in *Z. capensis*. For example, predation rates are generally thought to be high in the tropics and increased provisioning has been hypothesized to attract predators (Skutch 1949; Martin et al. 2000; Ghalambor & Martin 2001). Thus, it is thought that in tropical species with biparental care, selection will favor decreased provisioning rates where predation rates are high (Skutch 1949; Martin et al. 2000a, b; Ghalambor & Martin 2001). Previously studied *Z. capensis* populations in Papallacta, Ecuador appear to have high predation rates (Bonier pers. comm.). However, all nestlings of nests observed for this study (i.e., nests found with two eggs or nestlings) survived to fledge. Two nests with three nestlings were depredated (A. M. Class pers. obs.). If this relationship between provisioning and predation is real, we would expect males to trade time and energy invested in offspring provisioning for time and energy invested in increased background activity levels (e.g., flights or time in the perimeters of the territory). Male vigilance is a measure of background territorial activity levels, thus high vigilance scores may permit males to respond rapidly to potential threats, including conspecifics interested in extra-pair mating opportunities and/or potential predators. However, we did not observe a trade-off between vigilance and male provisioning, suggesting that high background activity levels do not directly impact time and energy spent on paternal provisioning.

Males that were not good providers may be spending time and energy pursuing extra-pair mates. While it has been proposed that extra-pair fertilization and thus extra-pair paternity (EPP) rates should be lower in the tropics (e.g., Stutchbury & Morton 2001; Spottiswoode & Moller 2004), a recent study on *Z. capensis* found that EPP rates were comparable to temperate congeners (Bonier unpub. data). We did not quantify EPP rates in this study, but suggest that males using this alternative tactic to increase fitness (as opposed to genetic monogamy) may gain considerable fitness benefits because fledging rates do not appear to depend on male provisioning rates (all nestlings in this study fledged, A. M. Class pers. obs.).

In temperate-zone breeding birds with male paternal care it makes sense that time and/or energy allotted to aggression would be negatively correlated with time and/or energy allotted to paternal care. Testosterone has been found to mediate male aggressive territory defense in the majority of species examined, to the detriment of paternal care (Wingfield et al. 1987; Wingfield et al. 1990; Wingfield et al. 2000; Lynn 2008). However, testosterone is not directly related to aggressive behavior in tropical *Z. capensis*. In fact, two studies found that 1) simulated territorial

intrusions did not lead to increased testosterone release in either the pre-breeding period or the nesting period, despite significant behavioral responses (Moore et al. 2004a) and 2) that blocking the action of testosterone did not effect territorial aggression responses to simulated territorial intrusion challenges (Moore et al. 2004b). Our data provide evidence that any direct time-energy trade-off between aggression and paternal care does not exist in *Z. capensis*. Thus, the typical hormone-behavior relationships of temperate-zone breeding birds do not appear to apply to tropical *Z. capensis*. Nevertheless, a recent study has shown that exogenous testosterone given to breeding male *Z. capensis* significantly diminishes paternal care (Lynn et al. 2009). Therefore, we suggest that males with higher than average testosterone, which may be useful for alternative pursuits such as responding to receptive extra-pair females, may not invest as much time and energy into provisioning their young. We suggest adult male *Z. capensis* may therefore have mixed strategies (Trivers 1974; Parker & Schwagmeyer 2005) of investing in current offspring, while also spending some time and energy investing in alternative tactics like securing extra-pair matings (Parker & Schwagmeyer 2005; Pryke & Griffith 2009). Future research examining which hormones control aggression responses and/or paternal care in the Las Caucheras population could greatly improve our understanding of trade-offs at both a proximate and ultimate level. Future research on selective forces influencing paternal behavior and mating systems in tropical species are also essential to our understanding of the ultimate causes of behavioral trade-offs.

Acknowledgments

We thank Los Flacos for permitting research on their land. We thank T.W. Small for logistical help throughout this project. Thanks to B.G. Freeman and H. Wada who provided valuable advice on manuscript drafts. Funding was provided from the National Science Foundation (IOS 0545735) and the Virginia Tech Graduate Research Development Program. The research described above adhered to animal care protocols by the IUCAC of Virginia Tech and Ecuadorian regulations.

Literature Cited

Ar, A. & Yom-Tov, E. 1978 The evolution of parental care in birds. *Evolution* **32**, 655-669.

- Atkins-Regan, E. 2005 *Hormones and Animal Social Behavior*. Princeton, NJ: Princeton University Press.
- Beletsky, L. D., Orians, G. H. & Wingfield, J. C. 1989 Relationships of steroid hormones and polygyny to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. *Auk* **106**, 107-117.
- Bortolotti, G. R. 1989 Factors influencing the growth of Bald Eagles in north central Saskatchewan. *Canadian Journal of Zoology* **67**, 606-611.
- Buckley, P. A., Foster, E. S., Morton, M. S., Ridgely, R. S. & Buckley, F. G. (ed.) 1985 *Neotropical ornithology*. Clutch size, nesting success and predation on nests of neotropical birds, reviewed. Washington DC, USA: American Ornithologists' Union.
- Busch, D. S., Wingfield, J. C. & Moore, I. T. 2004 Territorial aggression of a tropical passerine, *Zonotrichia capensis*, in response to a variety of conspecific intruders. *Behaviour* **141**, 1173-1188.
- Castro, G., Carey, C., Whittembury, J. & Monge, C. 1985 Comparative responses of sea level and montane rufous-collared sparrows, *Zonotrichia capensis*, to hypoxia and cold. *Comparative Biochemistry and Physiology* **82A**, 847-850.
- Chapman, F. M. 1940 The post-glacial history of *Zonotrichia capensis*. *Bulletin of the American Museum of Natural History* **77**, 381-438.
- Charnov, E. L. & Krebs, J. R. 1974 On clutch size and fitness. *Ibis* **116**, 217-219.
- Clotfelter, E. D., Chandler, C. R., Nolan, V. & Ketterson, E. D. 2007 The influence of exogenous testosterone on the dynamics of nestling provisioning in dark-eyed juncos. *Ethology* **113**, 18-25.
- Clutton-Brock, T. H. 1991 *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Constantini, D., Casagrande, S., Carello, L. & Dell'Omo, G. 2009 Body condition variation in kestrel (*Falco tinnunculus*) nestlings in relation to breeding conditions. *Ecological Research* **24**, 1213-1221.
- Davis, J. 1971 Breeding and molt schedules of the rufous-collared sparrow in coastal Peru. *The Condor* **73**, 127-146.
- Fotheringham, J. R. 1995 Differences in singing behavior between rufous-collared sparrows in Costa Rica and Northwestern Argentina. *The Condor* **97**, 821-826.

- Ghalambor, C. K. & Martin, T. E. 2001 Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**, 494-498.
- Greenlaw, J. S. & Post, W. 1985 Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: tests of hypotheses. *Animal Behaviour* **33**, 373-383.
- Hails, C. J. 1982 A comparison of tropical and temperate aerial insect abundance. *Biotropica* **14**.
- Hegner, R. E. & Wingfield, J. C. 1987 Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* **104**, 462-469.
- Janzen, D. H. 1973 Dissolution of mutualism between *Cecropia* and its Azteca ants. *Biotropica* **5**, 15-28.
- Jetz, W., Sekercioglu, C. H. & Böhning-Gaese, K. 2008 The worldwide variation in avian clutch size across species and space. *PLoS Biology* **6**, e303.
- Kalma, D. L. 1970 Some aspects of the breeding ecology and annual cycle of three populations of the rufous-collared sparrow (*Zonotrichia capensis*) in Western Panama, pp. 218. New Haven: Yale.
- Kendeigh, S. C. 1952 Parental care and its evolution in birds. *Illinois Biological Monographs* **22**, 1-356.
- Ketterson, E. D., Jr., V. N., Wolf, L. & Ziegenfus, C. 1992 Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *The American Naturalist* **140**, 980-999.
- Ketterson, E. D. & Nolan, V. 1994 Male parental behavior in birds. *Annual Review of Ecology and Systematics* **25**, 601-628.
- King, J. R. 1973 The annual cycle of the rufous-collared sparrow (*Zonotrichia capensis*) in three biotopes in northwestern Argentina. *Journal of Zoology, London* **170**, 163-188.
- King, J. R. & Hubbard, J. D. 1981 The comparative pattern of nestling growth in white-crowned sparrows. *Condor* **83**, 362-369.
- Klomp, H. 1970 The determination of clutch size in birds, a review. *Ardea* **58**, 1-124.
- Kokko, H. 1999 Cuckoldry and the stability of biparental care. *Ecology Letters* **2**, 247-255.
- Kokko, H. & Morrell, L. J. 2005 Mate guarding, male attractiveness, and paternity under social monogamy. *Behavioral Ecology* **16**, 724-731.

- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W.-C. 2001 Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour* **61**, 1029-1033.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Lofts, B. & Murton, R. K. 1968 Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *Journal of Zoology, London* **155**, 327-394.
- Lynn, S. E. 2008 Behavioral insensitivity to testosterone: Why and how does testosterone alter paternal and aggressive behavior in some avian species but not others? *General and Comparative Endocrinology* **157**, 233-240.
- Lynn, S. E., Prince, L. E., Schook, D. M. & Moore, I. T. 2009. Supplementary testosterone inhibits paternal care in a tropically breeding sparrow, *Zonotrichia capensis*. *Physiological and Biochemical Zoology*, *In press*.
- Marler, C. A. & Moore, M. C. 1988 Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology and Sociobiology* **23**, 21-26.
- Martin, T. E. 1996 Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**, 263-272.
- Martin, T. E. 2004 Avian life-history evolution has an eminent past: Does it have a bright future? *Auk* **121**, 289-301.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000a Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482-1485.
- Martin, T. E., Scott, J. & Menge, C. 2000b Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 2287-2293.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, I. T., Perfito, N., Wada, H., Sperry, T. S. & Wingfield, J. C. 2002 Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. *General and Comparative Endocrinology* **129**, 13-19.

- Moore, I. T., Wada, H., Perfito, N., Busch, D. S. & Wingfield, J. C. 2004a Territoriality and testosterone in an equatorial population of rufous-collared sparrows, *Zonotrichia capensis*. *Animal Behaviour* **67**, 411-420.
- Moore, I. T., Walker, B. G. & Wingfield, J. C. 2004b The effects of combined aromatase inhibitor and anti-androgen on male territorial aggression in a tropical population of rufous-collared sparrows, *Zonotrichia capensis*. *General and Comparative Endocrinology* **135**, 223-229.
- Morton, M. L. (ed.) 2002 *The mountain white-crowned sparrow: migration and reproduction at high altitude*. Cooper Ornithological Society Publication, Allen Press, Lawrence. Lawrence: Allen Press.
- Morton, M. L. & Carey, C. 1971 Growth and the development of endothermy in the mountain white-crowned sparrow (*Zonotrichia capensis oriantha*). *Physiological Zoology* **44**, 177-189.
- Newton, I. (ed.) 1972 *Finches*. London: Collins.
- Parker, G. A. & Schwagmeyer, P. L. 2005 Male "mixed" reproductive strategies in biparental species: Trivers was probably right, but why? *The American Naturalist* **165**, 95-106.
- Pryke, S. R. & Griffith, S. C. 2009 Socially mediated trade-offs between aggression and parental effort in competing color morphs. *The American Naturalist* **174**, 455-464.
- Ricklefs, R. E. 1969 An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* **9**, 1-48.
- Ricklefs, R. E. & Starck, J. M. 1998 Internal constraints on growth in birds. In *Avian growth and development: evolution within the altricial-precocial spectrum* (ed. J. M. Starck & R. E. Ricklefs), pp. 266-287. Oxford, UK: Oxford University Press.
- Ricklefs, R. E. & Wikelski, M. 2002 The physiology/life-history nexus. *Trends in Ecology & Evolution* **17**, 462-468.
- Ruiz, G., Rosenmann, M. & Novoa, F. F. 1995 Seasonal changes of blood values in rufous-collared sparrows from high and low altitude. *Journal of Biometeorology* **39**, 103-107.
- Sargent, M. B. & Gross, M. R. 1985 Parental investment decision rules and the Concorde fallacy. *Behavioral Ecology and Sociobiology* **17**, 43-45.

- Schoech, S. J., Ketterson, E. D., Nolan, V., Sharp, P. J. & Buntin, J. D. 1998 The effect of exogenous testosterone on parental behavior, plasma prolactin, and prolactin binding sites in dark-eyed juncos. *Hormones and Behavior* **34**, 1-10.
- Scriba, M. & Goymann, W. 2008 The decoy matters! Hormonal and behavioural differences in the reaction of territorial European robins towards stuffed and live decoys. *General and Comparative Endocrinology* **155**, 511-516.
- Silver, R., Andrews, H. & Ball, G. F. 1985 Parental care in an ecological perspective - A quantitative analysis of avian subfamilies. *American Zoologist* **25**, 823-840.
- Skutch, A. F. 1949 Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430-455.
- Smith, J. M. 1977 Parental investment: a prospective analysis. *Animal Behaviour* **25**, 1-9.
- Spottiswoode, C. & Moller, A. P. 2004 Extrapair paternity, migration, and breeding synchrony in birds. *Behavioral Ecology* **15**, 41-57.
- Stutchbury, B. J. M. & Morton, E. S. 2001 *Behavioral Ecology of Tropical Birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871-1971* (ed. B. Campbell), pp. 136-179. Chicago: Aldine Publishing Comp.
- Trivers, R. L. 1974 Parent-offspring conflict *American Zoologist* **14**, 249-264.
- Wada, H., Hahn, T. P. & Breuner, C. W. 2007 Development of stress reactivity in white-crowned sparrow nestlings: Total corticosterone response increases with age, while free corticosterone response remains low. *General and Comparative Endocrinology* **150**, 405-413.
- Wingfield, J. C. 1990 Hormonal control of territorial behavior in birds - field and laboratory investigations. In *Progress in Comparative Endocrinology* (ed. A. Epple, C. G. Scanes & M. H. Stetson), pp. 697-703. New York: Wiley-Liss, Inc.
- Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E. & Ramenofsky, M. 1987 Testosterone and aggression in birds. *American Scientist* **75**, 602-608.

- Wingfield, J. C., Hegner, R. E., Dufty, A. M. & Ball, G. F. 1990 The "Challenge Hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist* **136**, 829-846.
- Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S. L., Maney, D. L. & Soma, K. K. 2000 Toward an ecological basis of hormone-behavior interactions in reproduction of birds. In *Reproduction in Context. Social and Environmental Influences on Reproduction* (ed. K. Wallen & J. E. Schneider), pp. 85-128. Cambridge, MA, London: A Bradford Book, The MIT Press.
- Wolf, L., Ketterson, E. D. & Nolan, J. V. 1988 Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Animal Behaviour* **36**, 1601-1618.
- Wolf, L., Ketterson, E. D. & Nolan, J. V. 1990 Behavioural responses of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Animal Behavior* **39**, 125-134.
- Wolf, L., Ketterson, E. D. & Nolan, J. V. 1991 Female condition and delayed benefits to males that provide parental care: a removal study. *The Auk* **108**, 371-380.
- Zink, R. M. & Blackwell, R. C. 1996 Patterns of allozyme mitochondrial DNA, and morphometric variation in four sparrow genera. *The Auk* **113**, 59-67.

Table 3.1 Developmental characteristics by age class of nestling *Zonotrichia capensis*. We categorized *Z. capensis* nestlings into three age classes based on growth and developmental stages for *Zonotrichia* (Morton & Carey 1971; Morton 2002; Miller & Miller 1968).

| Age class | Age (days post-hatching) | Developmental characteristics |
|-------------|--------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Age class 1 | 1 – 3 | Nestlings are finishing eye development (eyes remain closed) and show their maximum (~logarithmic) increase in body size. |
| Age class 2 | 4 – 8 | Nestlings open their eyes, are increasingly alert and have coordinated movement. Nestlings transition from partial ectothermy to endothermy and will have gained nearly all of their adult body mass by age class 3. |
| Age class 3 | 9 – 12 | Nestlings are fully alert and will show escape behavior. Energy is primarily invested in feather production during this stage. |

Table 3.2 Principal component 1 (PC1) loadings for behavioral responses to simulated territorial intrusions in three nestling age classes.

| | PC1 loadings |
|----------------------------|--------------|
| Time within 5 m | 0.50 |
| Closest approach (m) | -0.51 |
| Number of songs | 0.53 |
| Number of song switches | 0.42 |
| Number of flights | 0.20 |
| Percent variance explained | 53.2 |

Principal component analysis was used to determine a single composite behavioral response variable, the ‘aggression score’, for each male. Mean aggression scores in each treatment group (nestling age class, age in days: age class 1, 1 - 3 days; age class 2, 4 - 8 days; age class 3, 9 - 12 days) were then compared.

Table 3.3 Provisioning rates vs. vigilance and aggression scores. Behavioral responses of territorial males to simulated territorial intrusions were compiled into a single individual behavioral score using principal components analysis. We then conducted linear regressions to determine whether the male and female provisioning rate (trips per hour) correlated with male vigilance scores and/or aggression scores in the three different age classes and among all age classes (age in days: age class 1, 1 - 3 days; age class 2, 4 - 8 days; age class 3, 9 - 12 days). Female provisioning rates were tested against the vigilance and aggression scores of their mates.

| | Vigilance score | | Aggression score | |
|---------------------------------|-----------------|----------|------------------|----------|
| | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> |
| Male provisioning rate | | | | |
| Age class 1 | -0.32 | 0.16 | 0.30 | 0.20 |
| Age class 2 | 0.21 | 0.42 | -0.36 | 0.10 |
| Age class 3 | 0.01 | 0.98 | -0.08 | 0.68 |
| All age classes | -0.03 | 0.84 | -0.03 | 0.83 |
| Female provisioning rate | | | | |
| Age class 1 | 0.15 | 0.56 | -0.45 | 0.07 |
| Age class 2 | 0.03 | 0.91 | 0.78 | 0.71 |
| Age class 3 | 0.17 | 0.56 | -0.10 | 0.71 |
| All age classes | 0.05 | 0.70 | -0.16 | 0.21 |

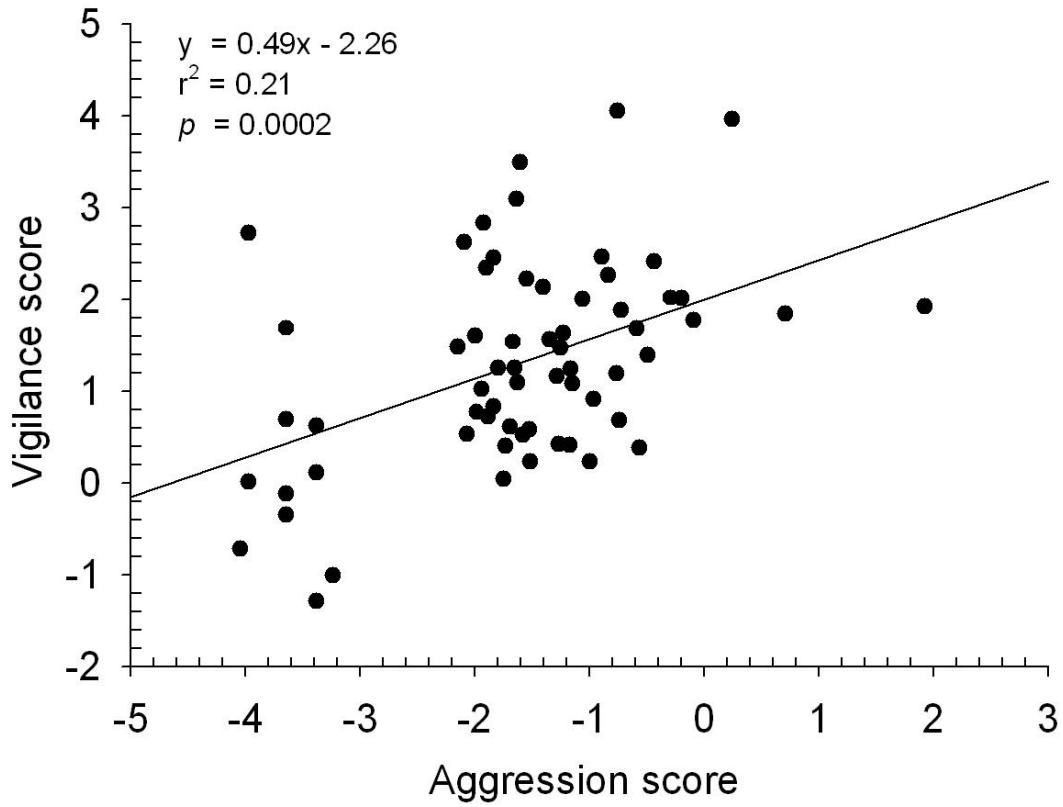


Figure 3.1 Relationship between vigilance and aggression scores of breeding territorial males. For explanation of the how scores were determined see methods.

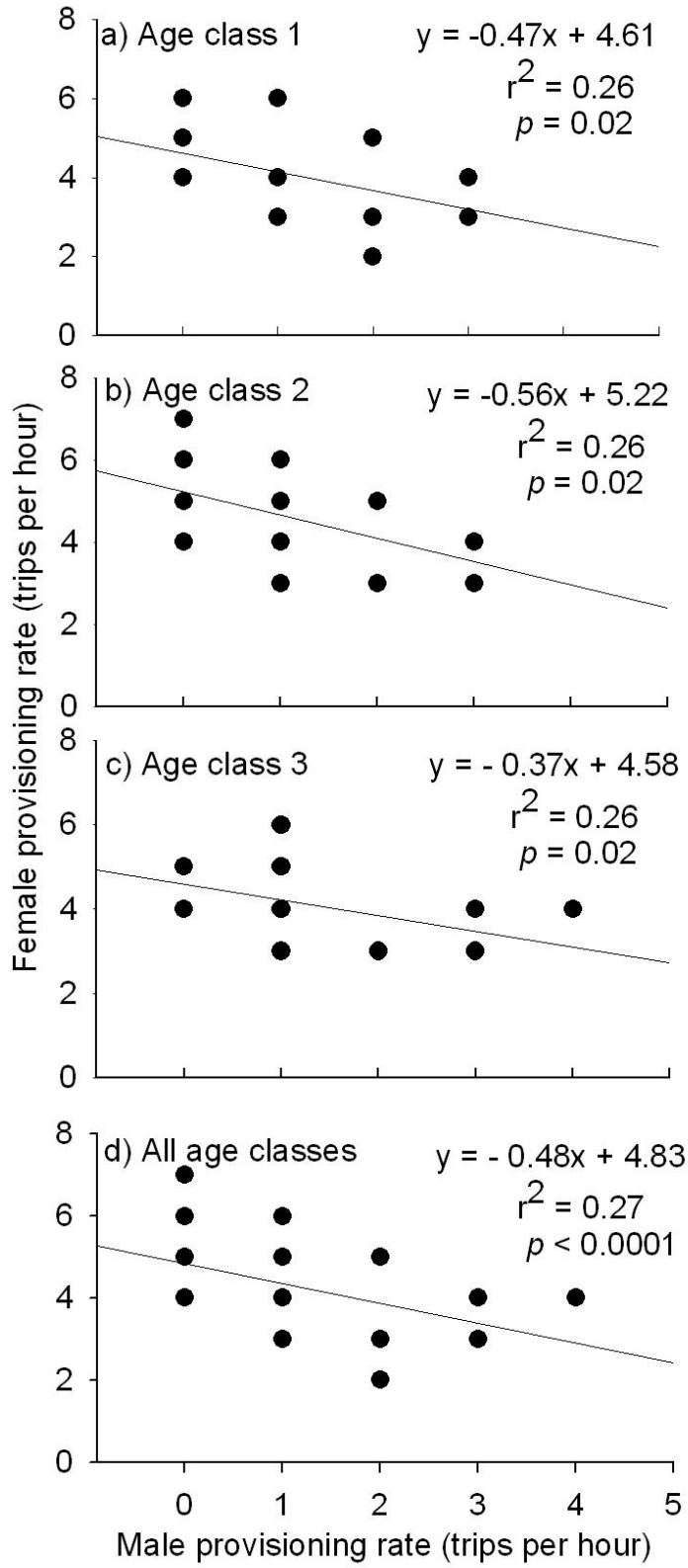


Figure 3.2 Relationship between female and male provisioning. The provisioning rate (trips per hour) for males versus females within pairs taken during one hour of observation are shown for each nestling age class (age in days): Age class 1, 1 – 3 days; Age class 2, 4 – 8 days; Age class 3, 9 – 12 days). See methods for additional information.

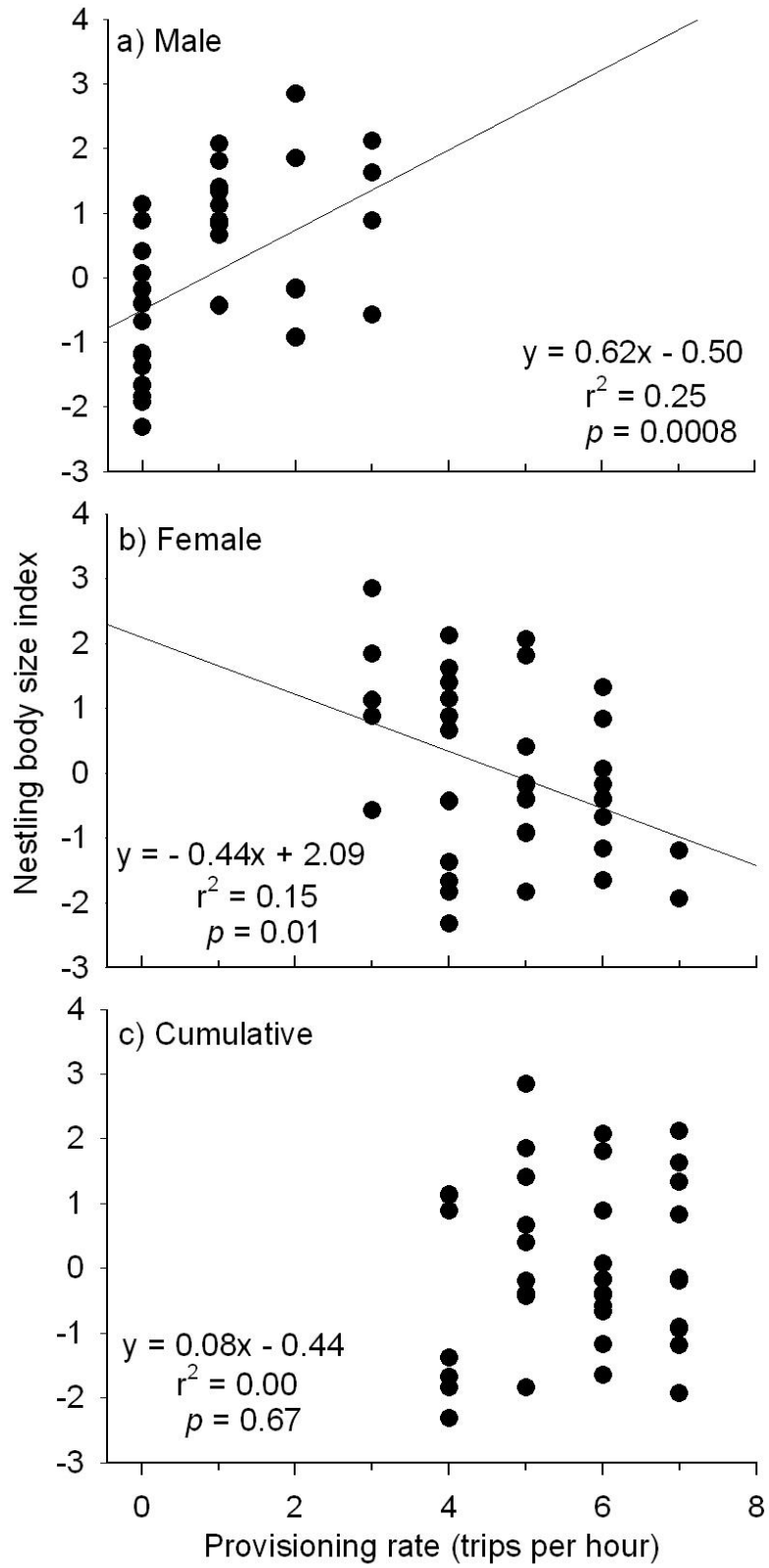


Figure 3.3 Relationship between nestling body size index and provisioning rate. The relationship between a) male b) female and c) cumulative provisioning rate (trips per hour) and nestling body size indices. Since measurements of nestling body size were only taken on 8 day-old nestlings (end of age class 2), we only used the provisioning rate observation from age class two. See methods for description of age classes and measurements as well as body size index calculation.

CHAPTER IV. FOOD SUPPLEMENTATION PROMOTES MOLT IN A TROPICAL BIRD

Alexandra M. Class and Ignacio T. Moore

Abstract

Tropical birds typically exhibit a 'slow pace of life' syndrome relative to their higher latitude counterparts. Characteristics of this syndrome include slow development, low fecundity and high survival. Following from this, it is predicted that individuals exhibiting the slow pace of life should trade current reproductive effort for maintenance, supporting survival and future reproduction. Recently, meta-analyses of food supplements studies in birds have found that food supplements typically advanced reproductive initiation and that the degree of advancement was negatively associated with latitude. However, there was only one tropical bird study included in these meta-analyses. We conducted two food supplementation experiments on tropical rufous-collared sparrows (*Zonotrichia capensis*) in the eastern Andes of Ecuador. In the first experiment, we supplemented territorial pairs during the non-breeding life history stage and in the second experiment we supplemented pairs that were provisioning fledglings. In both experiments food supplemented birds molted (replaced feathers) rather than investing further in reproduction. To our knowledge, this is the first study to experimentally demonstrate that a food supplemented bird invests in maintenance over reproduction. This result is consistent with a slow pace of life in the tropics and supports fundamental differences between temperate-zone and tropical *Zonotrichia*.

Introduction

According to life history theory, energy and time that could be invested in current reproductive effort may be traded-off for maintenance to increase individual fitness and survival (Charnov & Krebs 1974; Sterns 1976; Ghalambor & Martin 2001). These trade-offs may be particularly important to the timing of life history stages in less seasonal environments, like some tropical habitats (latitudes between the Tropic of Cancer and the Tropic of Capricorn, 23° 26'N, S, respectively) (Ricklefs & Wikelski 2002). In comparison to temperate-zone bird species, tropical bird species typically have slower development, lower fecundity and higher annual survival. This is the theoretical foundation for the syndrome of life history traits, collectively described as a 'slow pace of life', that is exhibited by many tropical bird species (Ricklefs & Wikelski 2002). Yet, little experimental evidence for the relationships among these variables exist, partially due to the difficulty in designing experimental studies that address these relationships and trade-offs (but see Ghalambor and Martin 2001). One way to begin to determine if life history trade-offs in tropical species are inherently different from those of temperate-zone species is to determine if there is a common response to a particular experimental manipulation across latitudes. Experiments augmenting food resources provide a means to investigate how species invest energy resources. It is presumed that individual birds will invest extra resources in the life history stage that garners the greatest fitness advantage.

In most studies of birds, experimentally increasing food abundance via supplementation typically results in advancing the initiation of reproduction (Arcese & Smith 1988; Kelly & VanHorne 1997; Aparicio & Bonal 2002; Scheuerlein & Gwinner 2002; Reynolds et al. 2003), while only a few studies show no effect of food supplementation on timing of reproduction (e.g. Korpimaki & Wiehn 1998; De Neve et al. 2004). Food supplementation has also been shown to increase the number of offspring per brood in some species (Yom-Tov 1974; Arcese & Smith 1988; Tinbergen & van Balen 1988) and/or increase the number of broods per breeding season (Davies & Lundberg 1984; Tinbergen & van Balen 1988; Nagy & Holmes 2005). However, the majority of data from food supplementation studies is derived from temperate-zone breeding bird species, where constrained timing of life history stages selects for any extra food resources to be invested directly into current reproduction. The vast majority of bird species breed in the tropics (~80% of all passerines) and have diverse social and territorial systems as well as life history strategies (Stutchbury & Morton 2001, 2008). Resident tropical birds are typically under less

temporal constraint to breed, thus they potentially have a more flexible breeding pattern than temperate-zone species (Lack 1954; Perrins 1970; Stutchbury & Morton 2008; Small & Moore 2009). Thus, resident tropical bird species are predicted to be more sensitive to supplemental feeding and to initiate reproduction more rapidly in response to food supplements than temperate-zone species (Schoech & Hahn 2007, 2008). This prediction is supported by recent meta-analyses of supplemental feeding studies, which show that food supplementation had a greater effect on advancing the initiation of breeding with decreasing latitude (Schoech & Hahn 2007, 2008). That is, birds from lower latitudes advanced breeding more in response to supplemental feeding than did birds from higher latitudes (Schoech & Hahn 2007, 2008). Yet these meta-analyses included data from only one tropical bird. Therefore, the hypothesis that the effect of food supplementation will be greater in tropical resident bird species than in temperate-zone breeding bird species remains essentially untested.

Bird species in the genus *Zonotrichia* range from the Arctic Circle to Tierra del Fuego, sea level to 5300 m altitude, and are comparably well-studied throughout their range (e.g., Chapman 1940; Blanchard 1941; Miller & Miller 1968; Moore et al. 2005). The rufous-collared sparrow, *Zonotrichia capensis*, is the only tropical congener of five species within the *Zonotrichia* genus, thus investigations of the species can add to our knowledge of tropical systems, while remaining within a well-studied genus and minimizing phylogenetic confounds that often hinder comparisons among tropical and non-tropical species. *Zonotrichia capensis* is a typical tropical bird, exhibiting a small clutch size and rarely multibrooding (Miller 1962; Miller & Miller 1968), while temperate-zone congeners have larger clutches and regularly multibrood during a single breeding season (Blanchard 1941; Morton 2002). The timing and duration of breeding and molting is highly variable in different *Z. capensis* populations. For example, in the Colombian Andes (~2000 m), *Z. capensis* can breed and molt biannually (Miller 1962), but in a high altitude population (~3300 m) in Papallacta, Ecuador, most individuals breed during a 3-month breeding season from September-November (Moore et al. 2005). In a preliminary examination of a mid-altitude population (~2100 m) in Ecuador, we found less reproductive synchrony, as breeding birds were caught during much of the calendar year (Class in prep). This population provided an excellent opportunity to determine if individuals allocate supplemental food for reproduction or maintenance, since reproduction did not appear seasonally constrained. We predicted birds fed food supplements would enter the nesting life history stage earlier than

controls given that they were investing food resources into reproduction. In birds, complete molt is an energetically costly maintenance period in which plumage is replaced which typically occurs once per year, but has been documented as occurring twice per year in a Colombian population of *Z. capensis* (Miller 1961). Thus, we predicted that if food supplements were invested into individual maintenance, birds would initiate molt (replace their plumage) more rapidly than controls.

Methods

Study site and species

The focal *Z. capensis* population inhabits the rural township of Las Caucheras in Napo province, Ecuador (0°39'S, 77°55'W; altitude ~2150 m). There is minimal change in photoperiod (~3 min) throughout the year (Bendix & Rafiqpoor 2001; Moore et al. 2005). Mean annual accumulated rainfall averages between 3150 – 3300 mm per year at this location. Though there is consistent high rainfall in Las Caucheras, monthly accumulated rainfall is between 130-240 mm from October-March and 280 – 390 mm from April-September (Instituto Nacional de Meteorológica, Ecuador). Mean monthly air temperature in Las Caucheras remains nearly constant throughout the year (~17° C; Instituto Nacional de Meteorológica, Ecuador). In the focal population, *Z. capensis* are sedentary and prefer habitat composed of natural and man-made humid-forest gaps, pasture, and cleared land in early stages of regeneration.

Assigning life history stages

We caught wild *Z. capensis* passively using mist nets from 8 December 2008 - 28 February 2009. Each bird was given a unique combination of three color bands and a uniquely numbered aluminum band. We measured reproductive morphology, molt (periodic replacement of feathers), and observed behavior of territorial residents to determine the life history stage of focal individuals (i.e., nesting, non-breeding, molting). To ensure we were assigning life history stages consistently, we set criteria by which we assigned life history stages to individuals (see Table 4.1 for details). Reproductive morphology included evaluating the female brood patch (developed to brood eggs and young), and length and width of the male cloacal protuberance (an extension of the cloaca used to deposit sperm during copulation). Cloacal protuberance size closely tracks testis volume in this species (Moore et al. 2005). We defined five brood patch stages in females: 1) defeathering, 2) defeathered, 3) edematous with hyperplastic epidermis (fluid-filled distended

skin pouch used for incubation), 4) refeathering, wrinkled/scaly skin, and 5) nearly refeathered (about 10% of growing feathers sheathed; flakey skin may still be visible). All captured birds were considered molting if one or more primaries were molting. We noted which primary and secondary flight feathers were molting and then used recaptures to describe the progression of all feather molt including body and rectrice molt.

Experimental design

We performed two experiments to determine how individuals allocated supplemental food. These experiments were performed on pairs of birds for which territory boundaries had been determined by a minimum of one hour of observation prior to the initiation of the experiments. In our first experiment, we provided food supplements to territorial *Z. capensis* that were in the non-breeding life history stage (hereafter *non-breeding experiment*). Pairs were identified as being in the non-breeding life history stage if they were captured without measurable reproductive morphology (brood patch or cloacal protuberance) and were not exhibiting reproductive behavior or molting for 5 – 6 weeks prior to the start of the experiment. In our second experiment (hereafter *feeding fledglings experiment*), we provided food supplements to pairs just starting to feed fledglings (young birds just out of the nest). Pairs that qualified for the feeding fledglings experiment were observed with either older nestlings or feeding young fledglings (pairs with nestlings 9 – 12 days old or young within 3 days of fledging). Every territory in both experiments, regardless of whether it was a control or experimental territory, received a feeder, but control territories did not receive food supplements. For the non-breeding experiment we set feeder stations on 30 territories (15 experimental, 15 control). For the feeding fledglings experiment, we set feeders on 34 territories (17 experimental, 17 control). We alternated assigning treatments to territories, but used the constraint that control territories had to be over 50 m from supplemental territories to minimize the occurrence of control birds eating food supplements.

Feeder stations and food supplements

Feeders were made of a covered wire-mesh cylinder attached to a platform base with adjustable ties and placed on an adjustable plastic pole. The wire mesh size permitted sparrow-sized birds access to food supplements, but made it difficult for larger animals to gain access to the food.

The food supplement mix consisted of unlimited mixed grass seed and approximately 12 freeze-dried mealworms per feeder per day (similar food was readily accepted by *Z. capensis* in another study, T. Small pers. comm.). To encourage territorial residents to come to feeders, seed was initially spread around the base of feeders and on the top of feeders. Individuals appeared to use feeders differently (e.g., some supplemented individuals were not observed entering feeders but fed on top of or on the ground around the feeder base, while others entered after a few days). Thus, we continued to place supplements on the ground immediately around feeder, on the top of feeders and inside of the feeders. To make the freeze-dried mealworms appear lifelike and shiny we reconstituted them by soaking them in vegetable oil. After feeders were set, we checked, observed and refilled feeder stations daily, the only exception being when there was severe inclement weather. To determine life history stages of territory holders, we mist netted throughout the day, rotating effort through all territories in approximately similar intervals to attempt to make observation and capture efforts uniform.

For both experiments we administered food supplements (to experimental groups) in feeder stations and observed territories (both control and experimental groups) for a total of 28 days per territory, beginning when we first observed territory residents eating the supplements (or when observations began for controls). However, we continued monitoring individuals past the initial 28 days to document transitions in life history stages.

Data analysis

We conducted a one-way analysis of covariance (ANCOVA) on change in mass (post experiment mass minus initial mass) of all recaptured individuals to determine if treatment had an effect on mass for both experiments, using treatment (supplemented or control) as a fixed effect and sex as a covariate (see Fig. 1 for mass differences of different sexes before and after treatment). Since measurable change in mass from food supplements may take several days to be detected, we only analyzed individuals that were recaptured between 14 and 44 days after the first day individuals were observed taking supplements (experimental territories), or, in the case of control territories, from when control feeders were set.

We conducted X^2 goodness-of-fit tests to examine the effects of treatment on life history stage. Since, at the onset of each experiment, individuals were in the same life history stage (all individuals in the non-breeding experiment were non-breeding), we used the life history stage of

individuals at time of recapture to analyze if treatment had influenced life history stage at the time of recapture. To ensure that sufficient time had elapsed from the onset of the experiment to cause a change in life history stage, we only used individuals recaptured during the same window of time described above (14 - 44 days, Fig. 4.2). To control for error in assigning individuals to life history stages, we excluded recaptures that were in states of transition, or individuals lacking sufficient observational data to determine the appropriate life history stage (e.g., where cloacal protuberance measured 3.0). We grouped recaptured birds with developing brood patches or enlarged cloacal protuberances into a general “breeding” category for analysis, as we did not necessarily know if these birds were in pre-breeding or nesting life history stages (i.e., if they were getting ready to breed, building nests, incubating, or with young).

Results

There was a significant effect of food supplements on individual mass gain in both experiments (non-breeding experiment: $F_{1, 27} = 112.64$, $p < 0.0001$; feeding fledglings experiment: $F_{1, 33} = 21.47$, $p = 0.02$). In the non-breeding experiment, supplemented individuals gained mass while control individuals did not gain mass (mass change \pm standard deviation: non-breeding control females (0.08 ± 0.58), non-breeding supplemented females (3.00 ± 0.91), non-breeding control males (-0.14 ± 0.64), non-breeding supplemented males (2.36 ± 0.56); Fig. 4.1a). In the feeding fledglings experiment, supplemented individuals also gained mass, while controls did not (mass change \pm standard deviation: feeding fledglings control females (-0.5 ± 0.5), feeding fledglings supplemented females (2.86 ± 1.34), feeding fledglings control males (0.21 ± 0.54), feeding fledglings supplemented males (2.58 ± 1.36 ; Fig. 4.1b). There were also significant differences in the proportion of life history stages at time of recapture between control and experimental treatments in both experiments (non-breeding experiment: χ^2 goodness-of-fit = 17.57, $df = 2$, $p = 0.0002$; feeding fledglings experiment: χ^2 goodness-of-fit = 17.89, $df = 2$, $p = 0.0001$). While the majority of controls stayed in the non-breeding life history stage in the non-breeding experiment and went into the non-breeding life history stage in the feeding fledglings experiment, the majority of supplemented individuals were molting when recaptured after the initiation of supplements (Fig. 4.2).

Discussion

To our knowledge, this is the first study to demonstrate that food-supplemented tropical birds invest in individual maintenance (via molting) over immediate reproduction. Our results suggest that molting may provide a greater increase in lifetime fitness than investing in current reproduction. Such a situation may be common in the tropics, where vertebrates exhibit a slower pace of life.

Feather molt in birds is the process of replacing old feathers which may be worn and inefficient. Fitness consequences of poor quality plumage can be substantial. Poor quality plumage can decrease flight efficiency (Metcalf & Ure 1995; Swaddle & Witter 1997), increase the risk of adult predation (Slagsvold & Dale 1996; Lind 2001) and increase the cost of thermoregulation (Walsberg 1988; Nilsson & Svensson 1996). Additionally, plumage quality is often a sexually selected trait, so having poor quality plumage can negatively influence reproductive success (Andersson 1986; Hill & McGraw 2006). Both molt and reproduction typically occur in periods of favorable resources, but are typically incompatible life history stages that do not overlap because both are energetically costly, taking considerable time and energy to complete (Murphy & King 1992; Murphy & Taruscio 1995; Nilsson & Svensson 1996; Ricklefs & Wikelski 2002; Rohwer et al. 2009).

Theory suggests that the order of life history stages is inflexible in vertebrates, but that the transition time between complete cycles of life history stages may vary more in species with fewer life history stages per annual cycle (for review see Jacobs and Wingfield 2000). Since our study population of *Z. capensis* is sedentary and tropical, it is suggested that they should transition between fewer life history stages during each life cycle relative to higher latitude congeners (Jacobs & Wingfield 2000). Reproduction, molt and non-breeding appear to be the main life history stages in our population. However, in ideal conditions individuals could potentially cycle between the two costly life history stages (reproduction and molt) twice per year as shown for *Z. capensis* in Colombia by Miller (1961). The non-breeding life history stage would therefore function as a transitional period where individuals recuperate or wait for the necessary resources to re-enter the reproduction-molt cycle. Our data provide support for this interpretation. In the feeding fledglings experiment, the majority of supplemented birds molted (59%), while most control birds entered the non-breeding stage (91%). This suggests that food

supplements may have helped to accelerate *Z. capensis* through the non-breeding life history stage and into the next costly life history stage, molt (Fig. 4.2).

Temperate-zone *Zonotrichia* and other emberizid sparrows often attempt multiple broods when resources are favorable (Blanchard 1941; Morton 2002). Further, food supplementation at the end of first broods can increase the number of broods attempted per pair per breeding season in emberizid sparrows (Arcese & Smith 1988). Thus, seasonally breeding temperate-zone bird species use highly abundant food resources during initial breeding attempts as a cue for how successful they could be at a subsequent brood. Though previous studies of *Z. capensis* suggest that molt typically occurs between breeding attempts (Miller & Miller 1968; Wolf 1968; Kalma 1970), our data did not cover a time period long enough to determine whether two breeding periods can occur without molt in between. Nevertheless, that the majority of control *Z. capensis* in the feeding fledglings experiment went into the non-breeding life history stage, suggests that control birds may have lacked adequate resources to molt. Instead control individuals transitioned to non-breeding (although one pair in this experiment did attempt another nest, demonstrating that double-brooding is possible).

The typical sequence of life history stages of tropical *Z. capensis* has been described as breeding to molting to non-breeding, then back to breeding again in populations other than Las Caucheras (Miller 1961, 1962; Miller & Miller 1968). Given that we found that a large proportion of feeding fledglings control individuals (91%) transitioned from reproduction (feeding fledglings) to the non-breeding life history stage, we suggest that individuals in Las Caucheras may enter transitional pauses between each of the more energetically expensive life history stages (molting and breeding). Thus, the life cycle would move from breeding to non-breeding to molting to non-breeding and again to breeding. Transitional pauses could serve as periods where individuals could evaluate their physiological condition prior to entering another expensive life history stage and/or wait for conditions to improve so that they could successfully complete the next life history stage.

In our non-breeding experiment, we tested if food supplements enabled birds to accelerate the transition into a costly life history stage (reproduction or molt). When we supplemented non-breeding individuals, nearly all supplemented individuals (83%) began molting, while most control birds (59%) remained in the non-breeding stage and a smaller percent (27%) of control birds molted (Fig. 4.2). We interpret our results as evidence that most

of our non-breeding individuals were in a transition period between reproduction and molt at the start of the experiment, and food supplements enabled them to begin molting. Unfortunately, we did not know the history of non-breeding individuals, which would be essential to be certain that the majority of individuals in the non-breeding experiment were transitioning from breeding to molt. Further, because the Las Caucheras population appears aseasonal, and the proportion of individuals in each life history stage throughout the year appears random (Class in prep), we expected an equal proportion of individuals should have been transitioning from molt to breeding as were transitioning from breeding to molt. A small number of individuals in both experimental ($n = 1$) and control groups ($n = 2$) bred during this experiment (Fig. 4.2). As expected, some individuals appear to have been transitioning from molt to reproduction. However, since the majority of birds molted in response to food supplements, it seems probable that in our study period most individuals had recently reproduced.

An alternative possibility is that some individuals may molt, enter non-breeding, then chose to molt again before breeding. While this seems unlikely, another molt (or partial molt) could greatly improve reproductive success prior to the next breeding period, especially if a transitional non-breeding period lasted a long time. Plumage quality deteriorates rapidly in *Z. capensis* due to habitat and climate (Miller 1961; Miller & Miller 1968) and reproductive success appears to be low in many tropical birds including *Z. capensis* (Skutch 1949; Miller & Miller 1968). Therefore, if poor plumage results in costs to future reproduction, it may be beneficial to molt before reproducing especially since there is no apparent seasonal constraint on the timing of reproduction (Miller 1961; Miller & Miller 1968). Tropical resident *Z. capensis* from Las Caucheras would be investing extra resources into the life history stage that is most critical to lifetime fitness (our data suggest molt) when resources become abundant, in this case. Physical condition may determine whether an individual enters into molt or breeding. However, individuals will not pass on any genes by continually molting, thus breeding should be favored over molt when individual condition is good enough to attempt breeding.

Most birds breeding in the temperate-zone reproduce in a single seasonal period, where a subsequent breeding opportunity is a year away and survival is unpredictable (Ghalambor & Martin 2001; Ricklefs & Wikelski 2002). In most temperate-zone breeding species breed when climate and resources are benign and there is a higher probability that reproduction will be successful. Therefore, experiments which have provided food supplements to birds prior to

breeding speed the transition into breeding and food supplements are invested into prolonging breeding or enhancing fecundity (Arcese & Smith 1988; Nagy & Holmes 2005; Schoech & Hahn 2007, 2008). Most individuals appear to have been transitioning from breeding to molt in the non-breeding experiment and all individuals were transitioning from breeding to molt in the feeding fledglings experiment in the Las Caucheras population. Providing food supplements may therefore have decreased the transition time into molt and into the subsequent breeding period as well. This supports previous studies of food supplemented birds, but shows a different effect in that birds were not transitioning into breeding, but into molt. We expect that temperate-zone and tropical breeding birds provided with food supplements immediately prior to molt may speed the transition time into molt as well. However, temperate-zone breeding birds have fixed time periods in which breeding can occur, thus molt can not be advanced indefinitely and experiments will be confounded by fixed seasonal annual cycles in hormones and behavior. Less seasonal tropical birds like *Z. capensis* in Las Caucheras may respond to food supplements according to their individual history and not a seasonal period synchronized to a specific time in the calendar year.

We show that food supplements in an equatorial population of *Z. capensis* promoted molting. The only other investigation using food supplements to test if food may be a cue for reproduction found supplements advanced the initiation of breeding in *S. torquata* by 36 days (Scheuerlein & Gwinner 2002). *Saxicola torquata* breeds in a defined breeding season (Scheuerlein & Gwinner 2002), unlike the focal population of *Z. capensis* (Class in prep.). Therefore, *S. torquata* given food supplements prior to their breeding season invest in immediate reproduction, similar to the results of food supplementation on temperate-zone birds. However, our results may be compatible with the results from *S. torquata*. By accelerating the onset of molt, the birds may eventually be accelerating the initiation of the subsequent breeding season. To determine this we would have had to let the experiment run longer. Responses of tropical birds to food supplementation may depend on their breeding seasonality and the time of the year in which food supplements are provided. It is possible that if food supplements were provided to individuals prior to breeding (if we knew the history of individual pairs and could estimate when the next breeding period would occur) that we could see the advancement of the initiation of breeding. Alternatively, individuals may chose to start molt after a period of non-breeding if feather wear is substantial and molting would greatly improve the chances that individuals

successfully complete the next breeding period. It is possible that a partial molt was initiated in some of the non-breeding supplemented individuals, but that our field period was not long enough to see individuals interrupt molt and enter breeding. In sum, the predictability of the onset and length of species' breeding periods and the period in which food supplements are provided will influence individual birds' responses to food supplements. More studies are needed on less synchronously and seasonally breeding tropical birds to clarify whether individual condition and history influence how supplemental food is invested in such conditions.

Acknowledgements

We thank SierrAzul and Los Flacos for permitting research on their land. We thank T.W. Small for help with finding materials and building feeder stations for this project. Thanks to B.G. Freeman, S. Rohwer, C. Eikenaar, and J. R. Moore who provided valuable advice on methodology, discussion topics and manuscript drafts. Funding was provided from the National Science Foundation (IOS 0545735) and the Virginia Tech Graduate Research Development Program and Sigma Xi. The research described above adhered to animal care protocols by the IUCAC of Virginia Tech and Ecuadorian regulations.

Literature Cited

- Andersson, M. 1986 Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* **40**, 804-816.
- Aparicio, J. M. & Bonal, R. 2002 Effects of food supplementation and habitat selection on timing of Lesser Kestrel breeding. *Ecology* **83**, 873-877.
- Arcese, P. & Smith, J. N. M. 1988 Effects of population density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology* **57**, 119-136.
- Bendix, J. & Rafiqpoor, M. D. 2001 Studies on the thermal conditions of soils at the upper tree line in the paramo of Papallacta (eastern cordillera of Ecuador). *Erdkunde* **55**, 257-276.
- Blanchard, B. D. 1941 The white-crowned sparrows, *Zonotrichia leucophrys*, of the Pacific Seaboard: environment and annual cycle. *University of California Publications in Zoology* **46**, 1-178.
- Charnov, E. L. & Krebs, J. R. 1974 On clutch size and fitness. *Ibis* **116**.
- Davies, N. B. & Lundberg, A. 1984 Food distribution and a variable mating system in the dunnock, *Prunella modularis*. *Journal of Animal Ecology* **53**, 895-912.

- De Neve, L., Soler, J. J., Soler, M. & Perez-Contreras, T. 2004 Nest size predicts the effect of food supplementation to magpie nestlings on their immunocompetence: an experimental test of nest size indicating parental ability. *Behavioral Ecology* **15**, 1031-1036.
- Ghalambor, C. K. & Martin, T. E. 2001 Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**, 494-498.
- Hill, G. E. & McGraw, K. J. (ed.) 2006 *Bird coloration* Cambridge, Massachusetts: Harvard University Press.
- Jacobs, J. D. & Wingfield, J. C. 2000 Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* **102**, 35-51.
- Kelly, J. F. & VanHorne, B. 1997 Effects of food supplementation on the timing of nest initiation in Belted Kingfishers. *Ecology* **78**, 2504-2511.
- Korpimäki, E. & Wiehn, J. 1998 Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* **83**, 259-272.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Lind, J. 2001 Escape right in moulting tree sparrows (*Passer montanus*). *Functional Ecology* **15**, 29-35.
- Martin, T. E. 1996 Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**, 263-272.
- Martin, T. E. 2004 Avian life-history evolution has an eminent past: Does it have a bright future? *Auk* **121**, 289-301.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000 Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482-1485.
- Metcalf, N. B. & Ure, S. E. 1995 Diurnal variation in flight performance and hence predation risk in small birds. *Proceedings of the Royal Society of London B* **261**, 395-400.
- Miller, A. H. 1961 Molt cycles in equatorial Andean sparrows. *The Condor* **63**, 143-161.
- Miller, A. H. 1962 Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **48**, 396-400.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, I. T., Bonier, F. & Wingfield, J. C. 2005 Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology* **16**, 755-762.

- Morton, M. L. (ed.) 2002 *The mountain white-crowned sparrow: migration and reproduction at high altitude*. Cooper Ornithological Society Publication, Allen Press, Lawrence. Lawrence: Allen Press.
- Murphy, M. E. & King, J. R. 1992 Energy and nutrient use during molt by white-crowned sparrows, *Zonotrichia leucophrys glambelii*. *Ornis Scandinavica* **23**, 304-313.
- Murphy, M. E. & Taruscio, T. G. 1995 Sparrows increase their rates of tissue and whole-body protein synthesis during the annual molt. *Comparative Biochemistry and Physiology a-Physiology* **111**, 385-396.
- Nagy, L. R. & Holmes, R. T. 2005 To double-brood or not? Individual variation in the reproductive effort in Black-Throated Blue Warblers (*Dendroica caerulescens*). *Auk* **122**, 902-914.
- Nilsson, J. A. & Svensson, E. 1996 The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**, 711-714.
- Perrins, C. M. 1970 The timing of birds' breeding seasons. *Ibis* **112**, 242-255.
- Reynolds, S. J., Schoech, S. J. & Bowman, R. 2003 Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. *Oecologia* **134**, 308-316.
- Ricklefs, R. E. & Wikelski, M. 2002 The physiology/life-history nexus. *Trends in Ecology & Evolution* **17**, 462-468.
- Rohwer, S., Ricklefs, R. E., Rohwer, V. G. & Copple, M. M. 2009 Allometry of the duration of flight feather molt in birds. *PLoS Biol* **7**, e1000132.
- Scheuerlein, A. & Gwinner, E. 2002 Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. *Journal of Biological Rhythms* **17**, 171-180.
- Schoech, S. J. & Hahn, T. P. 2007 Food supplementation and timing of reproduction: does the responsiveness to supplementary information vary with latitude? *Journal of Ornithology* **148**, S625-S632.
- Schoech, S. J. & Hahn, T. P. 2008 Latitude affects degree of advancement in laying by birds in response to food supplementation: a meta-analysis. *Oecologia* **157**, 369-376.
- Skutch, A. F. 1949 Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430-455.

- Slagsvold, T. & Dale, S. 1996 Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* **77**, 461-471.
- Small, T. W. & Moore, I. T. 2009 Seasonal neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding birds. *General and Comparative Endocrinology* **163**, 135-141.
- Sterns, S. C. 1976 Life-history tactics: a review of ideas. *Quarterly Review of Biology* **51**, 3-47.
- Stonehouse, B. 1962 The tropicbirds (genus *Phaethon*) of Ascension Island. *Ibis* **103B**, 124-161.
- Stutchbury, B. J. M. & Morton, E. S. 2001 *Behavioral Ecology of Tropical Birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- Swaddle, J. P. & Witter, M. S. 1997 The effects of molt on the flight performance, body mass, and behavior of European Starlings (*Sturnis vulgaris*): An experimental approach. *Canadian Journal of Zoology* **75**, 1135-1146.
- Tinbergen, J. M. & van Balen, J. H. 1988 Food and multiple breeding. *Acta International Ornithological Congress* **19**, 380-391.
- Walsberg, G. E. 1988 Heat flow through avian plumages: the relative importance of conduction, convection, and radiation. *J. Therm. Biol.* **126**, 211-222.
- Wiersma, P., Munoz-Garcia, A., Walker, A. & Williams, J. B. 2007 Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 9340-9345.
- Yom-Tov, Y. 1974 The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone L.*). *Journal of Animal Ecology* **43**, 479-498.

Table 4.1 Definition of life history stages. Characteristics and observations used to determine the life history stage of individuals. We checked all life history stage designations with behavioral observation of territorial pairs. See methods for description of brood patch scores (in parentheses) and cloacal protuberance measures.

| | |
|--------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Pre-breeding | Female with defeathering (1) or defeathered (2) brood patch or male with cloacal protuberance ≥ 2.5 mm and observed pair bonding (foraging and flying in close association, male often guarding female from intruders) and with nest material, constructing nest, or focal territory found with freshly lined nest. Captured without molting primary flight feathers. |
| Nesting | Female with fully edematous brood patch (for incubating eggs or nestlings), and/ or observed incubating eggs or feeding nestlings and/ or male with protuberance ≥ 5 mm length and not molting primary flight feathers. |
| Feeding fledglings | Observed feeding and following fledglings in or around defined territory and not molting primary flight feathers. |
| Molting | Caught with 1 or more primaries molting prior to experiment, recaptured with progressed molt or having completed molt post-experiment; male with cloacal protuberance ≤ 1 mm length; female without brood patch. |
| Non-breeding | Focal pair was not constructing a nest, incubating, nor feeding young. Male cloacal protuberance ≤ 1 mm length or female without brood patch and two or more of the following observations: not building a nest or incubating, not feeding fledglings, not molting any primary flight feathers. |

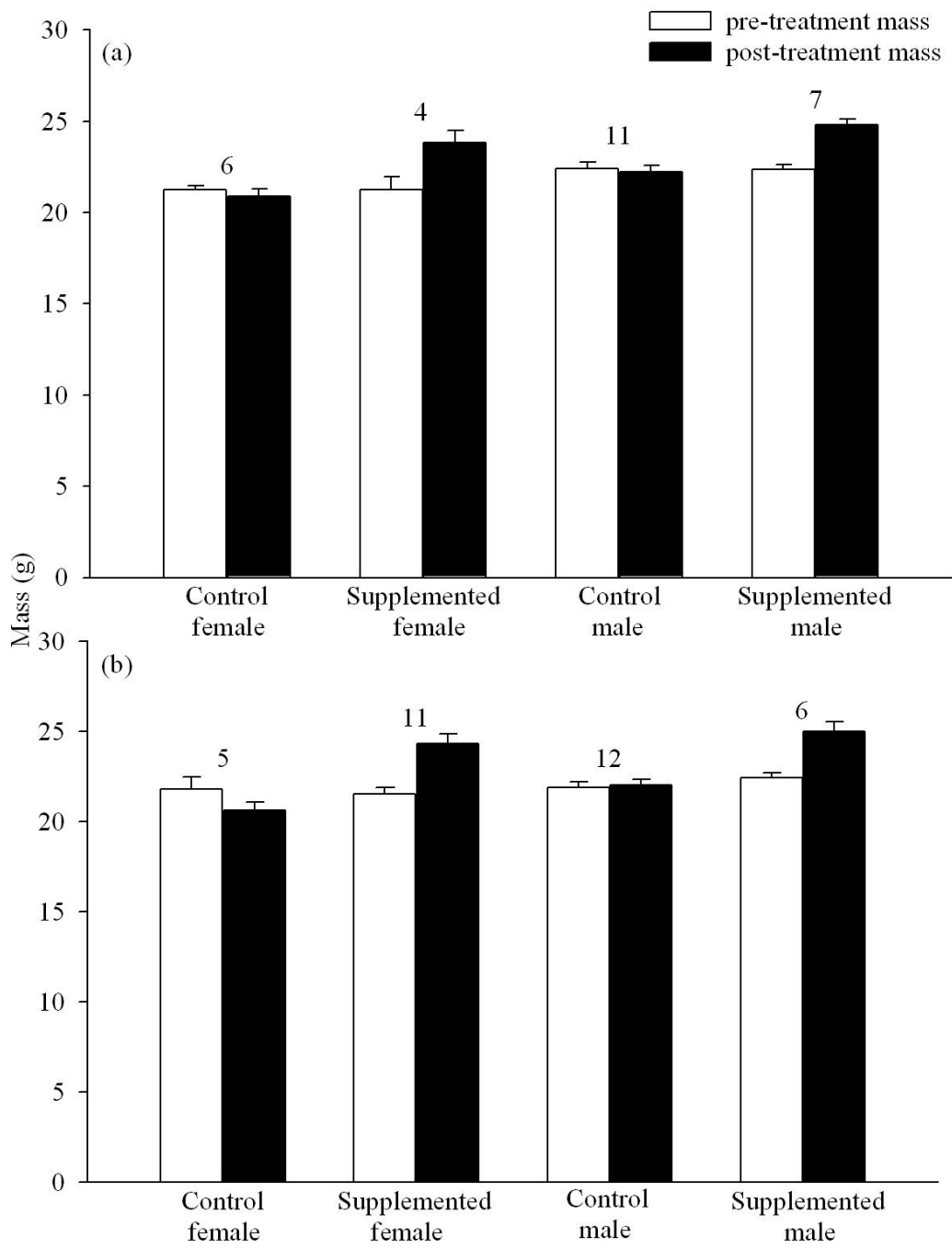


Figure 4.1 Mean mass (g) \pm SE pre- and post-treatment for focal individuals. Results for the non-breeding experiment are shown in (a) and for the feeding fledglings experiment in (b). Results are compared by sex and by control and supplemented treatments. Empty bars show pre-treatment mass measures and filled bars show post-treatment mass (either after supplementation for experimental birds or recapture mass for control birds). Sample sizes for the mass measures are provided above each bar pair.

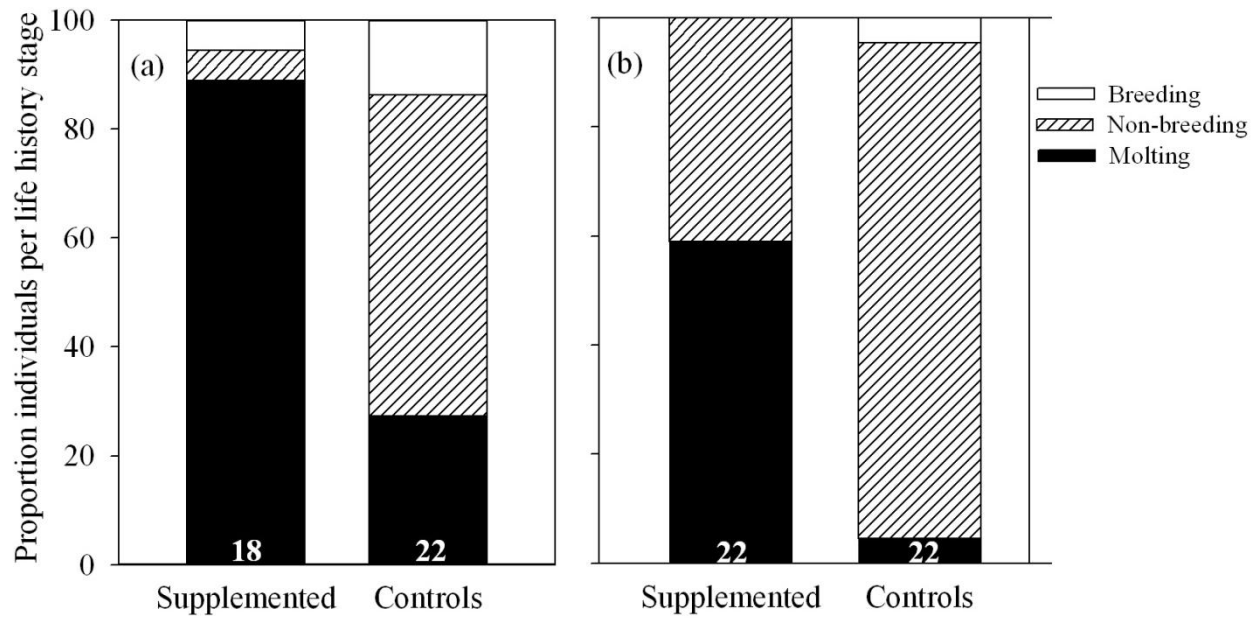


Figure 4.2 The proportion of individuals recaptured post-treatment in each life history stage in the (a) non-breeding experiment and (b) feeding fledglings experiment. Before each experiment, territories were assigned either control or experimental treatments (see methods for details). Individuals were then either provided food supplements (supplemented) or not provided supplements (controls). Sample sizes in each category are at the bottom of bars. See text for statistical results.

CHAPTER V. THE TIMING OF LIFE HISTORY STAGES ACROSS LATITUDES IN *ZONOTRICHIA* SPARROWS

Alexandra M. Class and Ignacio T. Moore

Abstract

Tropical vertebrates are considered to have more flexibility in the timing of life history stages than temperate species. However, the life history of most resident tropical species is poorly understood, making latitudinal comparisons of life history strategies difficult. We investigated the seasonality and synchrony of reproduction of an equatorial mid-altitude (~2100 m) population of rufous-collared sparrows (*Zonotrichia capensis*). We then compared our data with data from three other *Zonotrichia* populations across a range of latitudes and altitudes (total of two equatorial *Z. capensis* populations, one high and one mid-elevation, and two temperate-zone *Z. leucophrys* populations, one at high elevation and one at sea level). We hypothesized that: 1) temperate-zone bird species have greater population-level reproductive synchrony and seasonality than tropical species and 2) species breeding in high altitude environments have greater reproductive synchrony and seasonality than those at lower altitudes. In the mid-altitude tropical *Z. capensis* population we found no seasonal pattern in the proportion of adult life history stages exhibited at any given time. Comparisons among the several *Zonotrichia* populations revealed that temperate-zone *Zonotrichia* populations do not necessarily have higher reproductive synchrony or seasonality than tropical populations. In addition, tropical *Zonotrichia* populations altitude had a strong effect on seasonality but only weakly affected synchrony, while altitude appeared to have a large effect on seasonality and synchrony in temperate *Zonotrichia* populations. Thus, reproductive synchrony may be strongly influenced by altitude in addition to latitude.

Introduction

The seasonal timing of life history stages is typically shaped by the seasonality of the environment in which organisms have evolved. However, the ability of animals to make use of fluctuations in the environment to time life history stages depends on the predictability of seasonal fluctuations (i.e., do they occur at the same time each year?) and the amplitude of seasonal fluctuations (i.e., are changes detectible?) (Colwell 1974; Wingfield et al. 1992; Wingfield et al. 2000; Dawson 2008). Animals make use of environmental seasonality around the world to time annual cycles in behavior (Murton & Westwood 1977; Wingfield & Kenagy 1991). Seasonal reproduction is common in animals breeding in the temperate-zone (latitudes above or below Tropics of Cancer and Capricorn, 23°26'N, S respectively). Animals breeding in the temperate-zone time breeding seasons primarily by variation in photoperiod (day length), which influences seasonal temperature variation, and thus the availability of food resources (Baker 1938; Murton & Westwood 1977; Wingfield & Kenagy 1991; Deviche & Small 2001; Dawson 2002). Seasonal reproduction also is observed in tropical latitude species, but typically seasonal variation in precipitation, rather than temperature, is thought to be responsible for tropical breeding seasonality (Stutchbury & Morton 2001; Brown et al. 2002; Scheuerlein & Gwinner 2002). However, the interannual predictability of seasonal environmental fluctuation and the amplitude of seasonal fluctuation typically decline with latitude (Colwell 1974; Wingfield et al. 1992). That is, low latitude tropical environments tend to be defined by less predictable seasonal climate than high-latitude temperate-zone environments (Wingfield et al. 2000; Hau 2001; Stutchbury & Morton 2001; Dawson 2008).

Birds are well-studied compared to other taxa, but there is a strong research bias towards birds inhabiting the temperate-zone and considerably less research on tropical bird species (Stutchbury & Morton 2001, 2008). Though some tropical birds are migratory, most are non-migratory residents (Stutchbury & Morton 2001). Tropical birds are therefore believed to cycle between fewer life history stages (the two costly life history stages being reproduction and molt, the periodic replacement of feathers) (Jacobs & Wingfield 2000). Tropical birds existing in a less seasonal environment therefore have a wider window of time in which they can complete costly life history stages than the majority of temperate-zone residents (Jacobs & Wingfield 2000). Thus, tropical birds often show more variable timing of the initiation and/or termination of specific life history stages than temperate-zone breeding species (Stutchbury & Morton 2001;

Carvalho et al. 2006; Tori et al. 2007; Stutchbury & Morton 2008). However the vast majority of tropical species remain poorly studied, so comparisons among populations across latitudes remain difficult and are confounded by including species that have unique phylogenetic histories (Karr 1976; Martin 1996; Hau 2008; Stutchbury & Morton 2008).

Animal populations are often characterized and compared by their seasonality (O'Brian 1993; Stutchbury & Morton 2001; Brown et al. 2002; Dawson 2002). However, seasonality can be difficult to define, and often is assumed to be accurately portrayed by reproductive seasonality. The most widely used metric used to compare reproductive seasonality is the reproductive synchrony index, a measure of the proportion of simultaneously fertile females in a population (Birkhead & Moller 1992a, b; Kempenaers 1993). However, reproductive synchrony indices are not necessarily positively correlated with the breeding seasonality of a given population (Weatherhead & Yezerinac 1998). Thus, reproductive synchrony indices are most useful as indices of the tightness of fertile periods when several related populations are compared across altitudinal and latitudinal ranges.

Five species of *Zonotrichia* breed across a wide latitudinal and altitudinal range from northern Alaska (*Z. leucophrys*) to Tierra del Fuego, Argentina, (*Z. capensis*) and from sea-level to 5300 meters (Blanchard 1941; Bent 1968; Miller & Miller 1968; Morton 2002). *Zonotrichia* are numerous throughout much of their range and well-studied compared to other wild bird species. Thus, the genus *Zonotrichia* is a good candidate for investigations regarding seasonality and reproductive synchrony across a variety of environments. For the purpose of this investigation, we were concerned with data concerning two of the five subspecies: the white-crowned sparrow, *Zonotrichia leucophrys* and the rufous-collared sparrow, *Zonotrichia capensis*.

Breeding populations of *Z. leucophrys* exist in diverse habitat including coastal chaparral, city parks and subalpine meadows from Alaska through the southwestern United States (Blanchard 1941; Morton 1978). *Z. leucophrys* typically breed seasonally in the temperate-zone summer, but can be migratory or non-migratory depending on the subspecies (Blanchard 1941; Morton 2002). *Z. leucophrys* largely depend on an insect diet in spring and summer, but rely more on seeds in the winter (Morton 2002). Just as in the majority of temperate-breeding animals, *Z. leucophrys* uses photoperiod as the primary predictive cue for seasonal timing of reproductive physiology and behavior (Wingfield & Farner 1980; Wingfield & Moore 1987), but

each population may fine-tune seasonal reproductive timing with local changes in climate and/or food availability (Weathers et al. 2002).

Zonotrichia capensis is the only tropically ranging species in the genus *Zonotrichia* and is phylogenetically basal to the other *Zonotrichia* species (Zink & Blackwell 1996). Just as in other species of *Zonotrichia*, populations of *Z. capensis* exist in diverse habitats including coastal deserts, humid forest gaps, urban areas and páramo grasslands. The range of *Z. capensis* is from Chiapas, Mexico to Tierra del Fuego, Argentina (sea-level to 5300 m altitude). Over 20 subspecies of *Z. capensis* are recognized and cumulatively they demonstrate considerable variability in life history characteristics: they can be migratory or sedentary, eat a variety of seeds, insects and occasionally fruit, and have different temporal schedules for the timing and duration of life history stages (Chapman 1940; Miller & Miller 1968; Kalma 1970; King 1973; Moore et al. 2005). *Zonotrichia capensis* breed seasonally in several populations throughout their range: Costa Rica (Wolf 1969), Panama (Kalma 1970), Colombia (Miller 1959; Miller 1962), Ecuador (Moore et al. 2005), Peru (Davis 1971), Chile (Novoa et al. 1996) and Argentina (King 1973). However, seasonal timing of reproduction is variable among populations. For example, in the Colombian Andes, *Z. capensis* breed on a seasonal, but bimodal schedule (~2000 m) (Miller 1962), but in a high altitude (3300 m) population in Papallacta, Ecuador, most individuals breed during a 3-4 month breeding season from September to December (Moore & Wingfield 2002). Molting schedules also appear to follow either bimodal or unimodal seasonality in these two populations (Miller & Miller 1968, I. T. Moore unpub. data, respectively). Across their range all *Zonotrichia* are socially monogamous and generally exhibit biparental care.

We collected data from a focal population of a larger study of *Z. capensis* located at mid-altitude (~2100 m) in the rural township of Las Caucheras, Ecuador. In preliminary investigations of Las Caucheras we caught birds in molting or breeding condition throughout much of the calendar year (in prep), indicating less population-level seasonality of life history stages (Miller & Miller 1968; Moore et al. 2005). A primary aim of our investigations of Las Caucheras was describe the seasonality of life history stages throughout a calendar year of individuals in this population. To conduct a broad comparison among different *Zonotrichia* populations, we then compiled data on the reproductive timing of individual females from a high altitude equatorial *Zonotrichia* population (Lynn et al. 2009) and two temperate-zone *Zonotrichia* populations (one high altitude, one low altitude) (Wada et al. 2007; Wada & Breuner

2008). The hypotheses we tested using these data were that 1) temperate zone bird species have higher reproductive synchrony and seasonality than tropical species and 2) species breeding in high altitude environments have higher reproductive synchrony and seasonality than those at lower altitudes at the same latitude.

Methods

To investigate population-level reproductive synchrony we compared nesting data collected by investigators actively searching for nesting pairs of birds in four populations of *Zonotrichia* (refs. for relevant papers: Wada et al. 2007; Wada & Breuner 2008; Lynn et al. 2009). Each site was the subject of a larger study effort, thus researchers were familiar with the terrain and typical nesting habitat. All nest searching efforts were the major focus of investigations of reproductive behavior at the time researchers were actively searching for nesting pairs. Thus, data used to calculate reproductive synchrony indices were collected when detailed records of nests, nestlings, and fledglings (young out of the nest but still dependent on adults for food and protection) were kept.

Temperate Zonotrichia and study sites

We analyzed data from two temperate-zone *Z. leucophrys* populations. Data on nesting pairs, eggs, young and fledglings were collected during each populations' seasonally predictable breeding season, when the vast majority of all pairs were breeding. First, we analyzed data from a breeding population of *Z. leucophrys oriantha* in a subalpine meadow of the Sierra Nevada range near Tioga Pass, Mono County, California (37°55'N, 119°2'W, ~3000 m altitude) (collected in 2002; Wada et al. 2007). The seasonal climate at this location is characterized by a warm, dry period from May-September and cold temperatures with higher precipitation the remainder of the year, with the highest precipitation (snowfall) in December (Fig. 5.1).

Zonotrichia l. oriantha is an intracontinental migratory subspecies that breeds in montane habitat throughout the western United States and winters in mountains of the southwestern United States through southern Mexico and Baja California (Morton & Allan 1990). The breeding season typically begins in mid- to late May and continues through late July, though late-spring snowstorms can sometimes delay or terminate early nesting attempts (Morton et al. 1972; Morton & Allan 1990; Weathers et al. 2002). We also analyzed data from a *Z. l. nuttali*

population breeding in temperate-zone coastal lupine or chaparral habitats located around Bodega Bay Marine Laboratory on the California coast (38°27'N, 123°07'W, ~5 m) (data collected in 2005; Wada & Breuner 2008). *Zonotrichia l. nuttali* is the only non-migratory subspecies of *Z. leucophrys*. Similar to data collected from Tioga, data were collected on the nesting pairs during the single breeding season of *Z. l. nuttali* (late March – early August; Blanchard 1941; Baker et al. 1981). Bodega has predictable seasonal climate characterized by a warm, dry period from May – September, with higher precipitation and cooler temperatures the remainder of the year (Fig. 5.1).

Tropical Zonotrichia and study sites

We analyzed nesting data gathered from a seasonally breeding (September – December) *Z. capensis* population in Papallacta, Ecuador (0°21'S, 78°9'W, ~3300 m altitude) in the 2007 breeding season (Lynn et al. 2009). The temperature varies minimally throughout the year in Papallacta, but there is a defined rainy season from approximately March – August and a dry season from September – February (see Fig. 5.1; Bendix & Rafiqpoor 2001; Moore et al. 2005). In Papallacta there is also only ~3 min difference in photoperiod over the course of the calendar year, thus photoperiod may not be a meaningful cue for seasonal change in climate and resource abundance (Bendix & Rafiqpoor 2001, Moore et al, 2005). In Papallacta, *Z. capensis* are non-migratory inhabitants of grazing pastures and páramo grasslands. Only rarely have nests been found in other portions of the year (I. T. Moore unpub. data).

The majority of our research (on the seasonality of life history stages and reproduction) was primarily focused on a single population of tropical *Z. capensis*. This population consists of sedentary *Z. capensis* inhabiting the rural township of Las Caucheras in Napo province of Ecuador (0°37'S, 77°55'W; altitude ~2100 m). In this location, *Z. capensis* exist in natural and man-made humid-forest gaps, pasture, and early second-growth habitat. Mean annual accumulated rainfall averages between 3150 – 3300 mm per year and there is no dry season. Monthly accumulated rainfall is between 130 – 240 mm from October – March and 280 – 390 mm from April – September (Instituto Nacional de Meteorológica, Ecuador; Fig. 5.1). Mean monthly air temperature remains nearly constant throughout the year at ~17° C (Instituto Nacional de Meteorológica, Ecuador). Similar to Papallacta, Las Caucheras is very near to the equator, so it is likely that there is only minimal variation in photoperiod in Las Caucheras,

though photoperiod variation has not yet been measured in Las Caucheras. Since preliminary surveys of Las Caucheras indicated that breeding could occur year-round and did not appear seasonal, we collected data during two distinct periods of the calendar year to approximate the range of reproductive synchrony indices possible. We acknowledge that in populations such as Las Caucheras there is not a distinct seasonal period of breeding, so a large proportion of pairs will not be reproducing in one particular period of the year. However, we were interested in comparing the reproductive synchrony index of this population to the other populations for which we had data. Thus, we sampled the Las Caucheras population intensively for breeding pairs and nesting activity during two three-month periods in 2007 (14 March – 10 June and 8 September – 3 December).

Studying life history stages in Las Caucheras

The two field periods in Las Caucheras in 2007 were part of a broader study from 2004 – 2009 that investigated the timing of life history stages in the Las Caucheras population. In this broader study, we used mist-nets to capture wild birds. Upon capture, each bird received a unique combination of color bands and a uniquely numbered aluminum band. We also took morphological measures of each bird to collect data on the timing of life history stages at an individual and population level. Data from 2004 and 2005 were collected during a mist netting period of just a few days (14 – 17 December and 29 May - 2 June, respectively). However, the large majority of our data come from four separate field periods between 2006 and 2009. We scheduled field periods to sample as much of the calendar year as possible to examine the proportion of individuals in specific life history stages throughout the calendar year. Field periods covered 11 months of the calendar year in sum. There was one calendar month sampled in two field periods – we sampled from mid-May to mid-June in both 2006 and 2007. Each field period lasted approximately three months, and we divided each field period into three equal sampling periods (27 - 29 days each) to analyze seasonality of individual life history stages (see Fig. 5.2). Mist-netting effort was approximately equal in each three-month sampling period, but variable capture rates resulted in variable sample sizes for the sampling periods ($n = 21$ to 82).

Designating life history stages in Las Caucheras

In Tioga, Bodega and Papallacta sampling occurred when the majority of adult pairs were in the reproductive life history stage and the breeding seasons were known prior to study. In Las Caucheras it was essential to determine the life history stages of all captured and/or known individuals to examine the seasonality of life history stages because individuals were previously noted in all life history stages throughout the year. For each (re) captured individual we measured and scored reproductive morphology and molt (the periodic replacement of feathers). Our score of reproductive morphology included evaluating the brood patch (developed to brood eggs and young) for females, and length and width of the cloacal protuberance (an extension of the cloaca used to deposit sperm during copulation) for males. Cloacal protuberance size closely tracks testis volume in this species (Moore et al. 2005). We defined five brood patch stages in females: 1) defeathering, 2) defeathered, 3) edematous with hyperplastic epidermis (fluid-filled distended skin pouch used for incubation), 4) refeathering, wrinkled/ scaly skin, and 5) nearly refeathered (about 10% of feathers growing and sheathed; flakey skin may still be visible). Captured birds were considered to be in the molting life history stage if one or more primary flight feather was molting from each wing. However, to assess the progress of molt, the number and/or stage of individual feather molt for all primary and secondary flight feathers as well as for body and retrice (tail) feathers were recorded at each recapture. For the purpose of this study we categorized individuals captured from 2004-2009 into one of three life history stages: breeding, molting or non-breeding. Breeding birds were individuals recorded with active brood patches (scores from 1- 5) or cloacal protuberance length ≥ 5.5 mm and were not molting 1 or more primary flight feather on each wing. Birds categorized as molting were caught molting one or more primary flight feather on both wings and did not have brood patches or cloacal protuberances ≤ 2 . Non-breeding birds did not have brood patches or had cloacal protuberances ≤ 2 and were not molting 1 or more primary wing feather(s) in each wing. We excluded all juvenile birds from the analysis. We also excluded birds recaptured in less than 30 day interval and individuals that were in states of transition (i.e., where cloacal protuberance measured 3.5), to eliminate bias or error in assigning life history stages to individuals. The reproductive morphology measures described above also apply to the other populations (Papallacta, Bodega and Tioga), but since investigators knew the majority of pairs were breeding and since nest-searching was a primary objective, categorizing individuals was not essential.

Calculation of synchrony indices

Synchrony indices are a quantitative measure of how many females are simultaneously fertile (ready to breed) in a population at a given time (Birkhead & Moller 1992a, b; Kempnaers 1993). The most widely used formula for calculating the reproductive synchrony index of a given population was provided by Kempnaers (1993). The synchrony index formula is:

$$SI = \frac{1}{F} \sum_{p=1}^F \left[\sum_{i=1}^{t_p} f_{i,p} / t_p (F - 1) \right] \cdot 100$$

where F = total number of breeding females in the population

$f_{i,p}$ = number of fertile females, excluding female p , in the population on day i

t_p = number of fertile days for female p .

To calculate the synchrony index, one must know the date that the penultimate egg was laid by each female and an estimate of the females' fertile period. Where the date that the penultimate egg was laid is unknown (when nests are first found with full clutch of eggs or nestlings), morphological characteristics can be used to accurately age nestlings and to determine when the penultimate egg was laid (Kalma 1970; Miller & Miller 1968; Morton 2002). We then counted back to when the penultimate egg was laid, using the *Zonotrichia* incubation period of 12 days (Blanchard 1941; Miller & Miller 1968; Morton et al. 1972). We conservatively estimated a fertile period of eight days for all our populations, an estimate similar to fertile periods for passerines used in current literature (Birkhead & Moller 1992a; Lifjeld et al. 1997). We calculated synchrony indices using Kempnaers (1993) synchrony index for each of our four populations (independently for the two sampling periods in Las Caucheras). We also averaged the separate reproductive synchrony indices from the two separate Las Caucheras periods to approximate reproductive synchrony in general in Las Caucheras.

Tropical *Z. capensis* do not typically have multiple broods (attempt another brood immediately after a successful fledged first brood) or renest frequently (attempt another nest immediately after a failed nest) (Miller & Miller 1968). In the temperate-zone double brooding and renesting can occur (Weathers et al. 2002). Thus, in Bodega and Tioga populations we controlled for renesting by excluding any renesting attempt from our calculations of breeding

synchrony. To control for the possibility of multibrooding in the Bodega data set we included data only from the 18th of March (when the first nest was found) until May 1st (when the first second brood was attempted in this population in 2005). In Tioga, double brooding is occasional to rare and only occurs late in the nesting period. All data analyzed for this study were collected through mid-June and any noted second brood was excluded from the analysis, thus we believe the probability of multiple broods in the data set is minimal.

Results

Climate

We calculated means \pm SE for accumulated precipitation (cm) and temperature ($^{\circ}$ C) at each site over multiple years using available data (years of climate data analyzed: Bodega 6; Tioga 16; Las Caucheras 10; Papallacta 5). In both the Papallacta and Las Caucheras populations, mean monthly temperature fluctuated minimally throughout the year (Fig. 5.1). Seasonal shifts in precipitation are apparent in both Papallacta and Las Caucheras (Fig. 5.1). However, in Papallacta the rainy season is approximately from March through August, whereas the rainier season in Las Caucheras appears to go from April - October. While the seasonality is similar, the total rainfall is dramatically different – the peak mean monthly precipitation in Papallacta is nearly the same as the lowest mean monthly precipitation in Las Caucheras (Fig. 5.1).

In Tioga and Bodega populations there was a distinct seasonality in rainfall with peak levels of monthly precipitation (snow in Tioga) in December (Fig. 5.1). The change in seasonal temperature is more apparent in Tioga than any other site, demonstrated in an average temperature change of approximately 10° C from January to July (Fig. 5.1). Temperatures are less variable throughout the year in Bodega, with an increase in temperature ($\sim 4^{\circ}$ C) from July - August.

Population-level seasonality in Las Caucheras

We captured individuals in each life history stage in almost every calendar month of the year (Fig. 5.2). For example, we captured individuals in breeding condition in every sampling period but one (5 Nov - 3 Dec 2007). However, we found new nests and observed young juveniles during this sampling period, demonstrating that some individuals were indeed breeding.

Additionally, there did not appear to be any large seasonal peaks in any life history stage (see

Fig. 5.2). However, we did observe significant inter-annual differences in life-history stages in this population, as demonstrated by our one period of sampling overlap (mid-May to mid-June in both 2006 and 2007, Fig. 5.2). For example, we captured the highest proportion of breeding individuals and no molting individuals during this time in 2006. In comparison, we captured predominately non-breeding periods during this time in 2007, with some individuals also molting or breeding (Fig. 5.2).

Individual-level seasonality in Las Caucheras

Results are provided for 25 individuals that were captured in 2 or more field periods. Of the 25 individuals selected, 24 were individuals caught over 2 or more years (Table 5.1). Some recaptured individuals appeared to keep a similar schedule for certain life history stages over multiple years (e.g., individuals 12713 and 1523, Table 5.1). However, there was also considerable variability in the life history stage of individuals caught in the same portion of each year (e.g., compare individuals 1696, 1528 and 1524). We caught one individual (1541) breeding during three portions of the calendar year. We caught 3 individuals molting during 2 (possibly 3, in the case of 1710) separate periods in the same year.

Reproductive synchrony indices

We calculated synchrony indices from nesting data collected at each field site according to when populations were studied and/or when nests were found (see Table 5.2 for reproductive synchrony indices, details about sites, sampling period and sample sizes). Synchrony indices in the two tropical populations, were 19.2% in high altitude Papallacta and 13.8% (average of the two sampling periods) in mid-altitude Las Caucheras (Table 5.2). In comparison, temperate-zone reproductive synchrony indices were 17.1% in coastal Bodega and 43.4% in high-altitude Tioga (Table 5.2).

Discussion

Comparing seasonality using reproductive synchrony indices

Our data demonstrate a lack of correlation between synchrony and seasonality: the reproductive synchrony index for Papallacta is similar to the index for Las Caucheras, but the Papallacta population has a breeding season of approximately 3-4 months, while individuals in the Las

Caucheras population can breed in every month of the calendar year (Table 5.2). Moreover, Las Caucheras has a roughly equal synchrony index as the resident temperate-zone Bodega population. However, the Bodega population breeds during a single ~5 month season predicted by seasonal climate and driven principally by photoperiod, while Las Caucheras individuals appear not to rely on any single overarching climatic cue (Table 5.2). Our data therefore contradicts the hypothesis that latitude is a good predictor of reproductive synchrony and we suggest that factors like altitude and migratory status may better characterize reproductive seasonality. In sum, reproductive seasonality and synchrony are not necessarily interchangeable or highly correlated.

Factors affecting reproductive synchrony

It is proposed that where climatic and environmental cycles are highly predictable, there will be high seasonality in the timing of costly life history stages and therefore high reproductive synchrony of populations (Stutchbury & Morton 2001, 2008). Since temporal variability in both abiotic and biotic factors typically occur within more narrow time periods in the temperate-zone than in the tropics, it seems logical that the initiation of reproduction would occur within a narrower period at higher latitudes and potentially selecting for higher synchrony in female fertile periods. Indeed, breeding latitude is often discussed as an overarching factor explaining variation in reproductive synchrony, where decreasing latitude is thought to predict decreasing reproductive synchrony (Stutchbury & Morton 2001, 2008). However, our results suggest that latitude is not the primary driver of variation in reproductive synchrony in *Zonotrichia*.

In fact, reproductive synchrony indices calculated for socially monogamous birds show high variability even within birds reproducing in the temperate-zone (e.g., 17 to 70% synchrony of fertile females, excluding species breeding with mean breeding latitudes in the arctic circle) (Spottiswoode & Moller 2004). Very few studies have actually calculated reproductive synchrony indices for tropical bird species. Reproductive synchrony indices calculated for tropical species range from 8 - 30% (Spottiswoode & Moller 2004; Stutchbury & Morton 2008). Reproductive synchrony may be lower in the tropics, but there is considerable overlap in the range of reproductive synchrony between tropical and temperate-zone species. It is also worth noting that the commonly used method for a calculating reproductive synchrony index does not take into account the seasonality of a given population (Kempnaers 1993). Thus, in many

tropical populations of birds with extended breeding periods (or aseasonal breeding schedules) calculated reproductive synchrony indices will not take into account non-breeding adult females, which are members of the adult population and have the potential to breed, but were not reproducing during the period in which the population was sampled. This just reinforces our contention that the direct association of seasonality with synchrony is overly simplistic.

We suggest that breeding altitude may be a significant factor affecting reproductive synchrony because it affects the tightness of temporal schedules. Increasing altitude is associated with declining average temperature and declining primary productivity (Hahn et al. 2004; Bears et al. 2009). Populations of birds breeding in high altitude environments in both tropical and temperate latitudes may therefore have shorter windows of time in which successful reproduction can occur (Morton 1978; Morton 1994; Bears et al. 2009). We found a strong relationship between altitude and reproductive synchrony in temperate-zone *Zonotrichia*, but a weak relationship in tropical *Zonotrichia*. While increasing altitude is associated with an increasingly seasonal environment in tropical latitudes (Janzen 1967), seasonal resource fluctuations remain less pronounced in the tropics compared to the temperate zone. Additionally, our tropical populations are non-migratory. Migration, like altitude, confines reproductive timing, and this synergistic effect may explain why temperate-zone high altitude migratory birds (like our Tioga population, Fig. 5.2) have high reproductive synchrony. This has been shown to be the case in dark-eyed juncos (*Junco hyemalis*), where migratory populations breeding at high altitudes (2000 m) in the Rocky Mountains of Canada had shorter breeding seasons and higher reproductive synchrony than lower altitude (1000 m) non-migratory populations (Bears et al. 2009).

Seasonality of life history stages in a mid-altitude equatorial population, Las Caucheras

Data from our focal population in Las Caucheras shows variation in the timing of life history stages both at the level of the population and the individual. In Las Caucheras highly synchronized annual schedules of life history stages did not occur. Instead, individuals in all life history stages were found in nearly every calendar month; thus the population of *Z. capensis* in Las Caucheras is essentially aseasonal. In addition, we observed substantial inter-annual variation in the proportion of individuals in a given life history stage in the period in which sampling overlapped between years. Although there were no other sampling periods that overlapped, the high variation in the proportion of life history stages between May - June 2006

and 2007 suggests that there is high interannual variation in the timing of life history stages of individuals in Las Caucheras in general (Fig. 5.2).

Asynchrony in the temporal organization of life history stages in the Las Caucheras population suggests that no single overarching environmental factor is used to organize the timing of life history stages for the entire population. If such a factor existed, we would expect to see individuals respond to the factor in a similar fashion, creating measurable peaks in the number of individuals in a certain life history stage (e.g., breeding) at the same time. Instead, individuals recaptured from the Las Caucheras population demonstrated a diversity of temporal schedules that were neither synchronized across time nor with other individuals' schedules (Table 5.1). Though we cannot rule out the possibility that some individuals may have similar annual schedules over several years (e.g., individuals 12713 and 1523, Table 5.1), not all individuals recaptured over multiple seasons appeared to have similar schedules. Our data also demonstrate that temperature variation was minimal and neither the "rainy" period nor the "super-rainy" period in Las Caucheras corresponded to any particular life history stage (see Las Caucheras data Fig. 5.1 and 5.2). We suggest that the difference from rainy to super-rainy periods may not be strong enough to be detected or may not predictably determine a strong enough seasonal change in food resources to be used as a wide-scale cue for breeding.

Zonotrichia capensis is a dietary generalist and is known to eat a variety of insects, seeds and occasionally fruit, so while variation in rainfall may enable small peaks or declines in one or more type of food, the general availability of food may be similar across time (Miller & Miller 1968; Novoa et al. 1996). We therefore suggest that individuals in Las Caucheras respond to local abiotic and biotic fluctuations opportunistically, depending on their individual physiological condition, where pervasive environmental cues may not be consistent or permit an accurate prediction of resource cycles.

Conclusions

The assumption that tropical birds are less seasonal and therefore less synchronous is commonly suggested (Stutchbury & Morton 2008). However, socially monogamous tropical bird species show a range in reproductive synchrony indices that overlap with synchrony indices calculated for socially monogamous temperate birds. Additionally, broad comparisons of reproductive synchrony between temperate-zone and tropical species are typically not considered within a

phylogenetic framework, weakening the results of such comparisons. Our study, conducted within a phylogenetic framework, demonstrates that the relationship between reproductive synchrony and latitude is not simple, and other factors such as altitude and migratory status may affect synchrony to a greater extent.

Our estimates of the reproduction synchrony index from Las Caucheras are probably high because the formula for reproductive synchrony assumes that the majority of adult females in a population are reproducing within the confines of a breeding season (the period researchers have traditionally gathered data used to calculate reproductive synchrony indices). Populations without well defined or predictable breeding seasons will have a high proportion of individuals that are adults and capable of breeding, but may not breed at all during a given period. As a result of the assumptions of the synchrony index, namely that the population in question is a seasonally breeding population, our estimate is probably inflated and would be much lower if all adults capable of breeding were taken into account. Had we intensively sampled Las Caucheras over the course of an entire year, we would probably have better estimated the synchrony index.

We also caution that erroneous conclusions can also be reached simply by limited sampling, evidenced by our data. For instance, including data from just Las Caucheras and Bodega in our study would have led to an entirely different conclusion (e.g., that temperate-zone and tropical populations have similar synchrony indices) than sampling Papallacta and Tioga (e.g., that tropical and temperate-zone populations have very different reproductive synchrony indices). As more tropical and subtropical data are collected on breeding seasonality we will be able to attempt larger latitudinal comparisons of reproductive synchrony with phylogenetic control. We encourage the revising of useful metrics such as reproductive synchrony indices, so that reasonable comparisons can be made.

Acknowledgments

We are very grateful to Los Flacos, and la familia Luis for use of their lands. To Ursula Campos, Fernando Game, Bill Phillips and SierrAzul, your help in organizing lodging and logistics for the fieldwork critical to the success of this project and very much appreciated. Thanks to H. Wada and S. Lynn for sharing field data with us and providing suggestions for our comparisons. To M. Morton, J. R. Walters, C. Eikenaar your help and advice helped bring together early stages of this draft. To B. G. Freeman your moral support, help with figuring out analysis and proofing

this manuscript is much appreciated. We wish to acknowledge financial support from the National Science Foundation (IOS 0545735) and from Graduate Research and Development Program at Virginia Tech. The research described above adhered to animal care protocols by the IUCAC of Virginia Tech and Ecuadorian regulations.

Literature Cited

- Baker, J. R. 1938 The relation between latitude and breeding seasons in birds. *Proc. Zool. Soc. London* **108**, 557-582.
- Baker, M. C., Mewaldt, L. R. & Stewart, R. M. 1981 Demography of White-Crowned Sparrows (*Zonotrichia leucophrys* Nuttalli). *Ecology* **62**, 636-644.
- Bears, H., Martin, K. & White, G. C. 2009 Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. *Journal of Animal Ecology* **78**, 365-375.
- Bendix, J. & Rafiqpoor, M. D. 2001 Studies on the thermal conditions of soils at the upper tree line in the paramo of Papallacta (eastern cordillera of Ecuador). *Erdkunde* **55**, 257-276.
- Bent, A. C. 1968 The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific Seaboard: environment and annual cycle. *University of California Publication of Zoology* **46**, 1-176.
- Birkhead, T. R., Moller, A.P. (ed.) 1992a *Sperm competition in birds: evolutionary causes and consequences*. London: Academic Press.
- Birkhead, T. R. & Moller, A. P. 1992b Numbers and size of sperm storage tubules and the duration of sperm storage in birds -- A comparative study. *Biological Journal of the Linnean Society* **45**, 363-372.
- Blanchard, B. D. 1941 The white-crowned sparrows, *Zonotrichia leucophrys*, of the Pacific Seaboard: environment and annual cycle. *University of California Publications in Zoology* **46**, 1-178.
- Brown, G. P., Shine, R. & Madsen, T. 2002 Responses of three sympatric snake species to tropical seasonality in northern Australia. *Journal of Tropical Ecology* **18**, 549-568.
- Carvalho, C. B. V., Macedo, R. H. & Graves, J. A. 2006 Breeding strategies of a socially monogamous neotropical passerine: Extra-pair fertilizations, behavior, and morphology. *Condor* **108**, 579-590.

- Chapman, F. M. 1940 The post-glacial history of *Zonotrichia capensis*. *Bulletin of the American Museum of Natural History* **77**, 381-438.
- Colwell, R. K. 1974 Predictability, constancy, and contingency of periodic phenomena. *Ecology* **55**, 1148-1153.
- Davis, J. 1971 Breeding and molt schedules of the rufous-collared sparrow in coastal Peru. *The Condor* **73**, 127-146.
- Dawson, A. 2002 Photoperiodic control of the annual cycle in birds and comparison with mammals. *Ardea* **90**, 355-367.
- Dawson, A. 2008 Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 1621-1633.
- Deviche, P. & Small, T. 2001 Photoperiodic control of seasonal reproduction: neuroendocrine mechanisms and adaptations. In *Avian Endocrinology* (ed. A. Dawson & C. M. Chaturvedi). New Delhi, India: Narosa Publishing House.
- Hahn, T. P., Sockman, K. W., Breuner, C. W. & Morton, M. L. 2004 Facultative altitudinal movements by Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. *Auk* **121**, 1269-1281.
- Hau, M. 2001 Timing of breeding in variable environments: Tropical birds as model systems. *Hormones and Behavior* **40**, 281-290.
- Hau, M., Perfito, N., Moore, I.T. 2008 Timing of breeding in tropical birds: Mechanisms and evolutionary implications. *Ornitologia Neotropical* **19 (Suppl.)**, 39-59.
- Janzen, D. H. 1967 Why mountain passes are higher in the tropics. *The American Naturalist* **101**, 233-249.
- Kalma, D. L. 1970 Some aspects of the breeding ecology and annual cycle of three populations of the rufous-collared sparrow (*Zonotrichia capensis*) in Western Panama, pp. 218. New Haven: Yale.
- Karr, J. R. 1976 Seasonality, resource availability, and community diversity in tropical bird communities. *The American Naturalist* **110**, 973 - 994.
- Kempnaers, B. 1993 The use of a breeding synchrony index. *Ornis Scandinavica* **24**, 84-84.
- King, J. R. 1973 The annual cycle of the rufous-collared sparrow (*Zonotrichia capensis*) in three biotopes in northwestern Argentina. *Journal of Zoology, London* **170**, 163-188.

- Lifjeld, J. T., Slagsvold, T. & Ellegren, H. 1997 Experimental mate switching in pied flycatchers: male copulatory access and fertilization success. *Animal Behaviour* **53**, 1225-1232.
- Martin, T. E. 1996 Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**, 263-272.
- Miller, A. H. 1959 Reproductive cycles in an equatorial sparrow. *PNAS* **45**, 1095-1100.
- Miller, A. H. 1962 Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **48**, 396-400.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, I. T., Bonier, F. & Wingfield, J. C. 2005 Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology* **16**, 755-762.
- Moore, I. T. & Wingfield, J. C. 2002 Reproductive cycles in equatorial populations of rufous-collared sparrows, *Zonotrichia capensis*. *Integrative and Comparative Biology* **42**, 1281-1281.
- Morton, M. L. 1978 Snow conditions and the onset of breeding in the mountain white-crowned sparrow *Condor* **80**, 285-289.
- Morton, M. L. 1994 Comparison of reproductive timing to snow conditions in wild onions and white-crowned sparrows at high altitude *Great Basin Naturalist* **54**, 371-375.
- Morton, M. L. (ed.) 2002 *The mountain white-crowned sparrow: migration and reproduction at high altitude*. Cooper Ornithological Society Publication, Allen Press, Lawrence. Lawrence: Allen Press.
- Morton, M. L. & Allan, N. 1990 Effects of snowpack and age on reproductive schedules and testosterone levels in male white-crowned sparrows in a montane environment. In *Endocrinology of Birds: Molecular to Behavioral* (ed. M. W. e. al.), pp. 235-249. Berlin: Japan Sci., Soc. Press, Tokyo/Springer-Verlag.
- Morton, M. L., Horstmann, J. L. & Osborn, J. M. 1972 Reproductive cycle and nesting success of the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) in the central sierra nevada. *The Condor* **74**, 152-163.
- Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford, U. K.: Clarendon Press.

- Novoa, F. F., Veloso, C. & López-Calleja, M. V. 1996 Seasonal changes in diet, digestive morphology and digestive efficiency in the rufous-collared sparrow (*Zonotrichia capensis*) in central Chile. *The Condor* **98**, 873-876.
- O'Brian, G. 1993 Seasonal reproduction in flying foxes, reviewed in context of other tropical mammals. *Reproduction, Fertility and Development* **5**, 499-521.
- Scheuerlein, A. & Gwinner, E. 2002 Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. *Journal of Biological Rhythms* **17**, 171-180.
- Spottiswoode, C. & Moller, A. P. 2004 Extrapair paternity, migration, and breeding synchrony in birds. *Behavioral Ecology* **15**, 41-57.
- Stutchbury, B. J. M. & Morton, E. S. 2001 *Behavioral Ecology of Tropical Birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- Tori, W. P., Duraes, R., Ryder, T. B., Anciaes, M., Karubian, J., Macedo, R. H., Uy, J. A. C., Parker, P. G., Smith, T. B., Stein, A. C., Webster, M. S., Blake, J. G. & Loiselle, B. A. 2007 Advances in sexual selection theory: Insights from tropical avifauna, pp. 151-163. Maturin, Venezuela: Neotropical Ornithological Society, USGS Patuxent Wildlife Research Center.
- Wada, H. & Breuner, C. W. 2008 Transient elevation of corticosterone alters begging behavior and growth of white-crowned sparrow nestlings. *Journal of Experimental Biology* **211**, 1696-1703.
- Wada, H., Hahn, T. P. & Breuner, C. W. 2007 Development of stress reactivity in white-crowned sparrow nestlings: Total corticosterone response increases with age, while free corticosterone response remains low. *General and Comparative Endocrinology* **150**, 405-413.
- Weatherhead, P. J. & Yezerinac, S. M. 1998 Breeding synchrony and extra-pair mating in birds. *Behavioral Ecology and Sociobiology* **43**, 217-219.

- Weathers, W. W., Davidson, C. L., Olson, C. R., Morton, M. L., Nur, N. & Famula, T. R. 2002 Altitudinal variation in parental energy expenditure by white-crowned sparrows. *J. Exp. Biol.* **205**, 2915-2924.
- Wingfield, J. C. & Farner, D. S. 1980 Environmental and endocrine control of seasonal reproduction in temperate zone birds. *Progress in Reproductive Biology* **5**, 62-101.
- Wingfield, J. C., Hahn, T. P., Levin, R. & Honey, P. 1992 Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology* **261**, 214-231.
- Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S. L., Maney, D. L. & Soma, K. K. 2000 Toward an ecological basis of hormone-behavior interactions in reproduction of birds. In *Reproduction in Context. Social and Environmental Influences on Reproduction* (ed. K. Wallen & J. E. Schneider), pp. 85-128. Cambridge, MA, London: A Bradford Book, The MIT Press.
- Wingfield, J. C. & Kenagy, G. J. 1991 Natural regulation of reproductive cycles. In *Vertebrate Endocrinology: Fundamentals and Biomedical Implications*, vol. 4 (ed. P. K. T. Pawg & M. P. Schreibruan), pp. 181-241. San Diego: Academic Press, Inc.
- Wingfield, J. C. & Moore, M. C. 1987 Hormonal, social, and environmental factors in the reproductive biology of free-living male birds. In *Psychobiology of Reproductive Behavior: and Evolutionary Perspective* (ed. D. Crews), pp. 149-175. New Jersey: Prentice Hall.
- Wolf, L. L. 1969 Breeding and molting periods in a Costa Rican population of the Andean sparrow. *The Condor* **71**, 212-219.
- Zink, R. M. & Blackwell, R. C. 1996 Patterns of allozyme mitochondrial DNA, and morphometric variation in four sparrow genera. *The Auk* **113**, 59-67.

Table 5.1 Individual recaptured *Zonotrichia capensis*. The life history stage of individual *Z. capensis* recaptures were recorded over several years (2004-2009). We selected 25 individuals to compare inter- and intra-annual life histories because they demonstrated the range of the data collected and/or were recaptured several times. Each row represents an individual recaptured bird (denoted by band ID in the leftmost column) from Las Caucheras, Ecuador. The sex of individuals is shown in the second column. Months of the year are shown in the top row. Year of recapture is located to the right of each circle. We designated individuals as being in the breeding (filled circles), non-breeding (stippled circles), or molting (striped circles) life history stage. For life history stage designations see the methods. This table is a small subset of the population.

| ID | Sex | J | F | M | A | M | J | J | A | S | O | N | D |
|-------|-----|------|------|------|------|------|------|------|---|------|------|------|------|
| 12713 | F | | | ● 07 | | ● 05 | | | | | | | |
| | | | | | | ● 06 | | | | | | | |
| 1524 | F | | | | | ● 05 | | ● 06 | | | | | ● 04 |
| 1525 | F | | | | | ○ 06 | | ● 06 | | | | | ● 04 |
| 1541 | F | | | ● 07 | ⊗ 07 | ● 06 | | | | ● 07 | | | |
| | | | | | | ● 07 | | | | | | | |
| 1696 | F | | ● 09 | ○ 07 | | | | | | ● 07 | | | ● 08 |
| 1712 | F | | | ● 07 | | | | | | ● 07 | | | ⊗ 08 |
| 1733 | F | | | | ⊗ 07 | | | | | | | ⊗ 07 | ● 08 |
| 1735 | F | | | | ⊗ 07 | | | | | ● 07 | | | ● 08 |
| 1741 | F | | ⊗ 09 | | ○ 07 | | | | | ● 07 | | | |
| 1802 | F | ● 09 | | | | | | | | | ● 07 | | |
| 1504 | M | | | | | | ● 06 | | | | | | ● 04 |
| 1523 | M | | | ○ 07 | | ○ 07 | | | | ○ 07 | | | ⊗ 08 |
| 1528 | M | | | | | | ○ 05 | | | | | | |
| | | | | | | | ● 06 | | | | | | |
| 1577 | M | | | | ○ 07 | | ● 06 | | | ● 07 | | | |
| 1703 | M | ⊗ 09 | | ○ 07 | | | | | | | ⊗ 07 | | ⊗ 08 |
| 1710 | M | | | ○ 07 | | ○ 07 | | | | ○ 07 | | | ⊗ 08 |
| 1717 | M | | | ○ 07 | | ○ 07 | | | | | | | ○ 08 |
| 1729 | M | | | | ○ 07 | | | | | | ● 07 | | ⊗ 08 |
| 1740 | M | | ○ 09 | | ○ 07 | | | | | ● 07 | | | ⊗ 08 |
| 1756 | M | | ● 09 | | ● 07 | | | | | ⊗ 07 | | | |
| 1758 | M | ● 09 | | | | ○ 07 | | | | | | ⊗ 07 | ○ 08 |
| 1769 | M | | ⊗ 09 | ○ 07 | | | | | | ⊗ 07 | | | |
| 1775 | M | | | ○ 07 | | | | | | | | ○ 07 | ● 08 |
| 1786 | M | | | | | ● 07 | | | | | ● 07 | ○ 07 | ○ 08 |
| 1809 | M | | | | | ⊗ 07 | | | | | ● 07 | ⊗ 07 | |

Table 5.2 Synchrony indices for four *Zonotrichia* populations (according to Kempenaers 1993).

| Study Site | Species | Sampling period | Days spent nest searching | Nests found | Synchrony index | Latitude | Altitude (m) | Migratory status |
|-------------------------|-------------------------------|-------------------------|---------------------------|-------------|-----------------|----------|--------------|------------------|
| Tioga, California, USA | <i>Z. leucophrys oriantha</i> | 1 May – 20 Jun 2002 | 27 | 36 | 43.4% | 37°55'N | 3000 | Migratory |
| Bodega, California, USA | <i>Z. leucophrys nuttali</i> | 1 Apr – 30 Jun 2007 | 54 | 78 | 17.1% | 38°27'N | 5 | Resident |
| Papallacta, Ecuador | <i>Z. capensis</i> | 25 Sept – 5 Nov 2007 | 43 | 20 | 19.2% | 0°21'S | 3300 | Resident |
| Las Caucheras, Ecuador | <i>Z. capensis</i> | 14 Mar – 10 Jun 2007 | 88 | 15 | 9.6% | 0°36'S | 2100 | Resident |
| Las Caucheras, Ecuador | <i>Z. capensis</i> | 8 Sept – 3 Dec 2007 | 86 | 28 | 18.0% | 0°36'S | 2100 | Resident |
| Las Caucheras, Ecuador | <i>Z. capensis</i> | averaged periods (2007) | 174 | 43 | 13.8% | 0°36'S | 2100 | Resident |

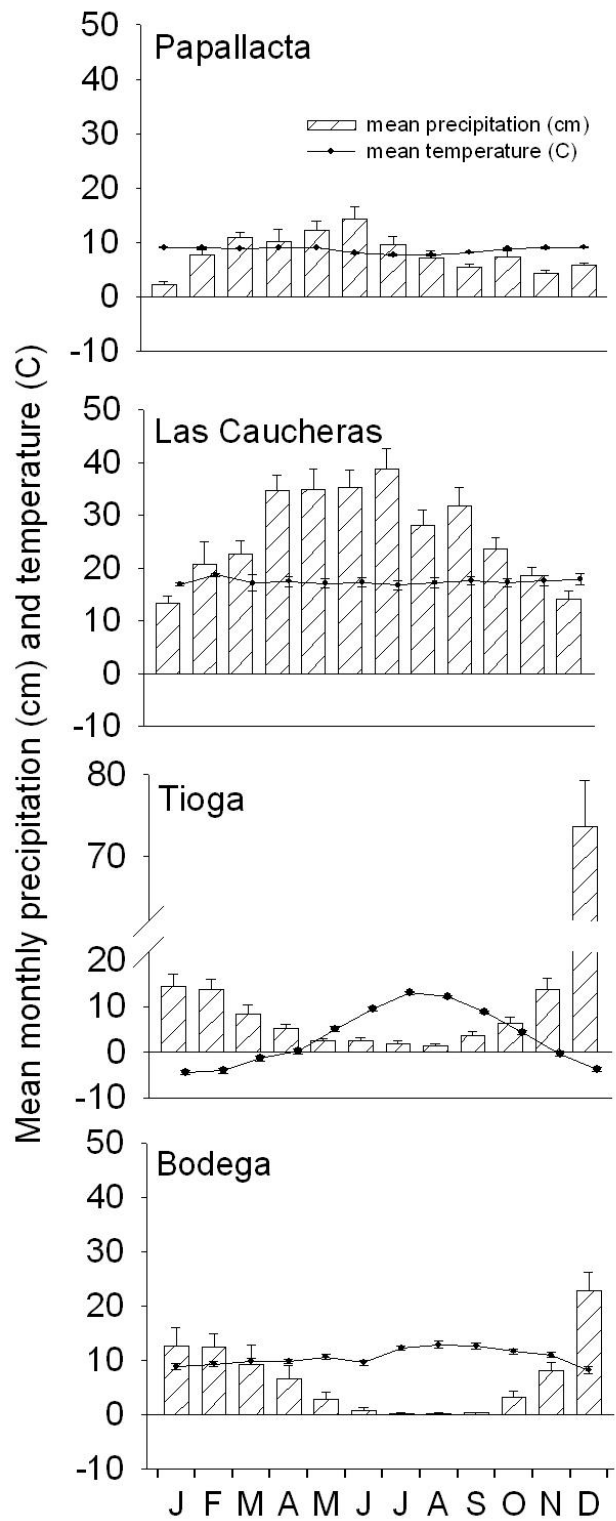


Figure 5.1 Climate data from the four field sites. Mean \pm SE monthly temperature ($^{\circ}\text{C}$) and mean \pm SE monthly accumulated precipitation (cm) for Papallacta (2002 - 2007), Las Caucheras (1982 - 1992), Tioga (1992 -2008) and Bodega (2002 - 2008) field sites. Data from weather stations nearby were used to approximate climate at the site in two cases. At the tropical field sites Papallacta data were collected at the field site, but we used data from the nearest weather station at the town of Cosanga (approximately 8 km away) to approximate the climate for the Las Caucheras. For temperate-zone field sites, we approximated the climate at Tioga with data collected from the Tuolumne weather station (approximately 10 km from the Tioga field site), while the Bodega weather station was situated at the Bodega field site. For details and data ranges see methods. Data provided by I. T. Moore (Papallacta), Instituto Nacional de Meteorología, Ecuador (Las Caucheras); University of California, Davis, Bodega Marine Laboratory, <http://bmlsc.ucdavis.edu/boon/index.shtml> (Bodega); Tuolumne Meadows weather station, Yosemite National Park (Tioga).

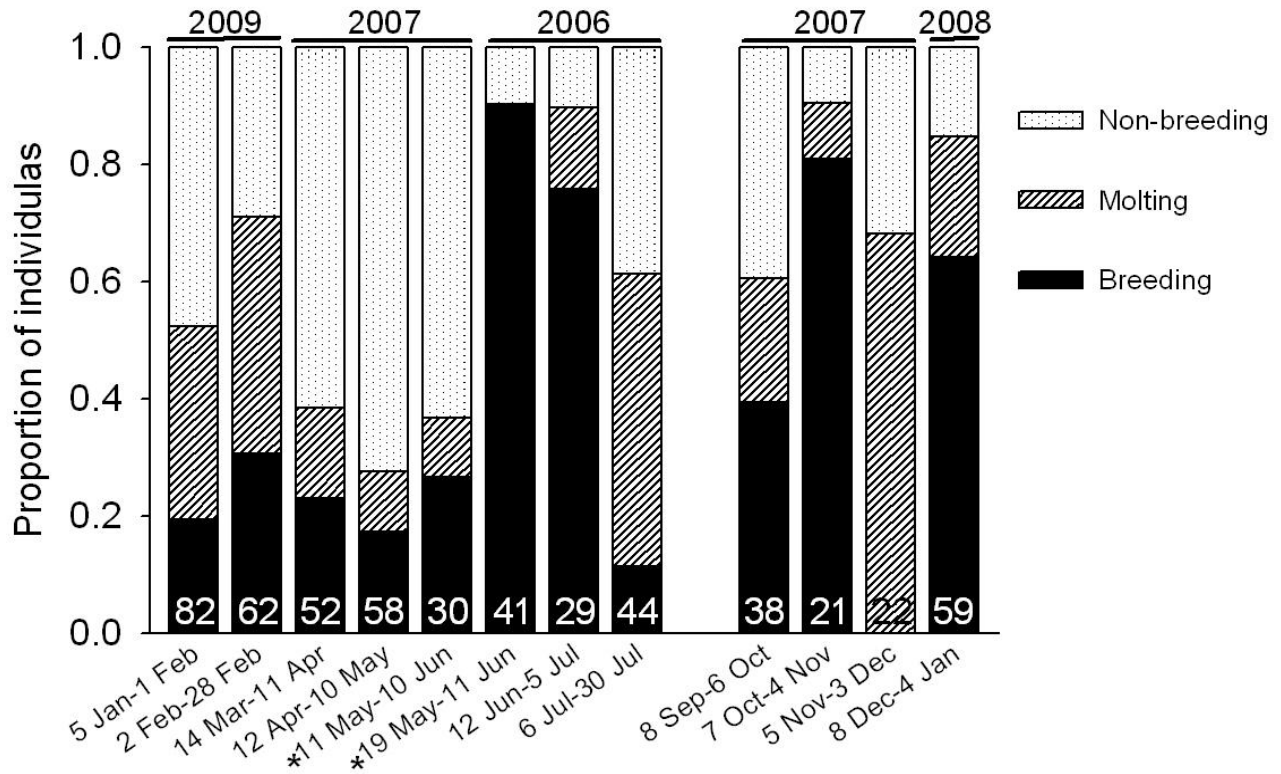


Figure 5.2 Life history stages of *Z. capensis* captured throughout the calendar year. Proportions of captured birds assigned to breeding, molting, or non-breeding life history stages are shown in each bar. Sampling periods are given below each bar and sample sizes are shown at the base of each bar. The year in which months of sampling occurred is designated by a horizontal line above bars at the top of the figure. Note that two sampling periods overlap (May – June 2006 and 2007; distinguished with asterisks). Not all individuals captured could clearly be assigned to one of the life history stages, thus this is a subset of total captures. See methods section for detail on how date ranges and life history stages were designated.

CHAPTER VI. LOW AMPLITUDE SEASONALITY AND TRADE-OFFS BETWEEN MOLT AND BREEDING LIFE HISTORY STAGES IN EQUATORIAL RUFOUS- COLLARED SPARROWS, *ZONOTRICHIA CAPENSIS*

Las Caucheras population-level seasonality

Several features of the Las Caucheras (0°37'S, 77°55'W) study population of rufous-collared sparrows (*Zonotrichia capensis*) suggest that strong population-level synchronizing cues are absent. This is most notably demonstrated by the high degree of asynchrony of life history stages within the population. This level of asynchrony has only rarely been described in nature, as the majority of temperate-zone and also tropical breeding bird populations show distinct seasonal cycles, where reproduction, molt and/ or migration occur in a specific window of time (Baker et al. 1940; Moreau et al. 1947; Lofts & Murton 1968; Murton & Westwood 1977; Wingfield et al. 1992; Dawson et al. 2001; Hau 2001; Stutchbury & Morton 2008). In environments with low seasonality, physiological condition, individual history and social cues within monogamous pairs of *Z. capensis* may be the most important determinants of the timing of individual life history stages. Thus, the timing of life cycles (a complete cycle of life history stages) will be more variable, with pairs relying predominantly on social synchronizing cues to time life history stages (Jacobs & Wingfield 2000; Small & Moore 2009). This perspective is supported by data from the chapters of my dissertation and by previous research (e.g., Stonehouse 1962; Ashmole 1963; Hau et al. 2008; Perfito et al. 2008; Hahn & MacDougall-Shackleton 2008) investigating how animals time life cycles in environments with low amplitude seasonality.

Cue response systems and timing life cycles to the environment

In the absence of strong population-level synchronizing cues, endogenous rhythms may become more influential in timing life cycles. Endogenous rhythms are internal rhythms that vary in duration, cycle continuously without external cues and are typically synchronized to the environment by a *zeitgeber*, or external cue. Tuning endogenous rhythms to a *zeitgeber* allows life history stages to be timed appropriately to environmental or social conditions (Lofts & Murton 1968; Gwinner 1996; Gwinner 2003; MacDougall-Shackleton & Hahn 2007; Hahn & MacDougall-Shackleton 2008; Wikelski et al. 2008). The most predictable and universal cue used to time life cycles with regard to changes the environment is photoperiod (day length).

Therefore, cue response systems have evolved to respond to photoperiod as the zeitgeber (MacDougall-Shackleton & Hahn 2007; Hahn & MacDougall-Shackleton 2008; Wikelski et al. 2008).

Most environments, including tropical environments, are to some degree seasonal (Lofts & Murton 1968; Murton & Westwood 1977; Hau 2001; Stutchbury & Morton 2001). However, in the temperate-zone (latitudes above or below Tropic of Cancer and Capricorn 23°26' N, S, respectively) photoperiod strongly correlates with seasonal changes in temperature and food availability, which can be used to predict optimal resource-rich periods for breeding (Lofts & Murton 1968; Murton & Westwood 1977). A species' 'photoperiodic drive' is a measure of how responsive a species is to photoperiodic change (Follett & Nicholls 1984; Nicholls et al. 1988). Photoperiodic drive can be used predict how important other cues are in timing life cycles (Follett & Nicholls 1984; Nicholls et al. 1988). Species breeding in arctic latitudes, such as arctic-breeding *Zonotrichia* species, have high photoperiodic drive (Nicholls et al. 1988). Therefore, the influence of supplementary cues (e.g., food availability) and synchronizing cues (e.g., social stimuli) are considered to be secondarily important to photoperiod (Nicholls et al. 1988). The high photoperiodic drive of high-latitude breeders is adaptive because seasonal environmental changes are profound and periods suitable for breeding are short-lived, thus precise timing of breeding is critical to individual fitness and survival (Lofts & Murton 1968; Murton & Westwood 1977; Nicholls et al. 1988). However, as breeding latitude decreases, photoperiod decreases and so does the degree of temperature variation, leading to less profound seasonality in the environment. Though some low-latitude birds can perceive small photoperiodic changes in the wild (e.g., Hau et al. 1998), birds breeding at mid- or low-latitude typically show lower photoperiodic drive. Therefore, mid- to low-latitude breeding bird species are predicted to have high responsiveness to cues other than photoperiod (Follett & Nicholls 1984; Nicholls et al. 1988; Hau 2001).

Factors influencing aseasonality in bird populations

In some tropical environments birds may abandon seasonal timing determined by external cues because seasonal environmental change may be minimal or may not accurately predict a period of the year that is significantly more favorable for any single life history stage (Ashmole 1963; Chapin 1954; Hau 2001; Stonehouse 1962). Las Caucheras is essentially on the equator, and

therefore photoperiod change may be indiscernible (~3 min change annually in a high altitude population at the same latitude; Bendix & Rafiqpoor 2001; Moore et al. 2004). Additionally, average daily temperature is virtually constant throughout the year (Chapter V). There is a seasonal shift in precipitation from high precipitation (rainy) to higher precipitation (super-rainy) periods in Las Caucheras, but no apparent correlation of seasonal rainfall with population-level life history stages (Chapter V). Further, the timing of precipitation is considered to be most predictive of seasonal food availability in xeric environments, or environments where heavy rains are infrequent (Boag & Grant 1984; Hau et al. 2004; Strand et al. 2007; Perfito et al. 2008). Overlap in sampling effort of the study population (during one month) revealed completely different proportions of the population in each life history stage during different years (Chapter V). Cumulatively, this suggests that there is no selection for any single life history stage to occur at a particular time of the calendar year in Las Caucheras. Highly aseasonal populations, such as Las Caucheras, are very rare (Hau 2001; Stutchbury & Morton 2001; Hau et al. 2008). However, aseasonality is also known in many populations of tropical seabirds (Chapin 1954; Stonehouse 1962; Ashmole 1963).

Low amplitude environmental seasonality, individual history, and competition for resources may select for population-level asynchrony of life cycles. Tropicbirds (*Phaethon sp.*) breeding on Ascension Island and frigatebirds (*Fregata sp.*) breeding on Aldabra Atoll may breed year-round (Stonehouse 1962; Diamond 1975). Tropicbirds breeding on Ascension Island, in the Atlantic Ocean (7°57'S; 14°22'W) experience low amplitude environmental seasonality, with fish prey appearing to be consistently available throughout the year, permitting year-round breeding (Stonehouse 1962). In the Aldabra Atoll, in the Indian Ocean (9°24' S; 46°22' E), dry and wet seasons may partially explain peaks in breeding in frigatebird colonies (owing to shifts in prey availability and habitat conditions on the island), but frigatebirds can also breed year-round (Diamond 1975). On both islands there is high inter- and intra-specific competition for nesting sites leading to high rates of egg destruction, nestling mortality, and consequently repeat nesting (Stonehouse 1962; Diamond 1975). Thus, strong density dependent selection and individual history, along with the low environmental seasonality permitting year-round breeding lead to population asynchrony (Stonehouse 1962; Diamond 1975).

In another case, red-billed tropicbirds (*Phaethon aethereus*) breeding on nearby islands within the Galapagos Archipelago (0°50'S; 90°30'W), in the Pacific Ocean, are either seasonal

or aseasonal breeders depending on the island (Snow 1965; Harris 1969). On one hand, South Plaza Island is a small island with dispersed nest sites, and is occupied by a small *P. aethereus* breeding population, defined by seasonal peaks in breeding (though singular records of nesting birds have been found all times of the year) (Snow 1965; Harris 1969). Aseasonal breeding is the norm on larger, more densely populated Daphne Major Island, though it is only 16 miles distant (Harris 1969). Similar to the tropicbird and frigatebird colonies on Ascension Island and Aldabra Atoll (discussed above), the larger colony on Daphne Major Island also had high nestling mortality and high renesting rates. Therefore, Snow (1965) suggested that density dependent selection overrides any weak seasonal peak(s) in fish food availability. It is possible that in some populations of *Z. capensis*, including Las Caucheras, where strong environmental seasonality is absent and populations are densely inhabited, density dependent selection may influence population asynchrony. If there is a period of the year that may be slightly more favorable for breeding, it could be the case that higher competition for resources during this period may lead to increased mortality of offspring and adults. Moreover, the rate of predation may depend on the ability of predators to predict periods when nesting is high. Thus, if slightly more pairs initiated nests in one portion of the year than another, it could be that mortality from predation dampens any selective advantage gained by higher resource availability. Unlike tropical seabird colonies breeding on islands, terrestrial *Z. capensis* habitat is largely contiguous, and new habitat (from the destruction of forested land and increase in agriculture) is increasingly available, so it seems less likely that populations are as limited by nesting habitat, as in the case of Ascension and Daphne Major Island tropicbirds.

Timing life cycles to less than a year

Species' life cycles can occur in periods less than one year in duration when the majority or entirety of the year provides favorable resources for energetically demanding life history stages, such as breeding and molt (Chapin 1954; Miller 1961, 1962; Ashmole 1963; Miller & Miller 1968; Diamond 1975). The general strategy of individual pairs in such populations should be to breed as much as possible, taking individual physiological condition and history into account. For instance, individual *Z. capensis* have been observed completing two life cycles per year, with life cycles occurring at ~6 month intervals in Colombia (3°50'N, 76°70'W) (Miller 1961; 1962; Miller & Miller 1968). Biannual life cycles in Colombian *Z. capensis*, could be timed via two

periods of high rainfall, separated by short dry seasons roughly from January - March and July - August, when the majority of birds stop breeding and begin molt (Miller 1962; Miller & Miller 1968). In the Colombian population of *Z. capensis*, strong biannual changes in rainfall may be enough to permit endogenous cycles of 6 months to be roughly synchronized with to seasonal rainfall and/ or associated cues (Miller 1961, 1962; Miller & Miller 1968). *Zonotrichia capensis* residing in Colombia can complete two life cycles per year because 1) there is no period of the year when temperature ultimately constrains breeding and/ or molting, unlike in temperate-zone environments and 2) because much of the calendar year is suitable for breeding and/ or molt.

Individuals were recorded in the breeding or molting life history stage in two distinct periods within one year in the Las Caucheras population (Chapter V). Unfortunately, individual data from Las Caucheras are inconclusive regarding whether two complete cycles of breeding and molt occurred for any individual in the course of one year. Las Caucheras *Z. capensis* experience lower environmental seasonality – characterized by a lack of a dry period – than all previously studied populations, including those in Colombia (Miller & Miller 1968; Wolf 1969; Kalma 1970; Davis 1971; King 1973; Moore et al. 2005; Chapter V). Nevertheless, breeding and molt take similar amounts of time to complete in Las Caucheras as they do in Colombia, where life cycles can occur twice a year (Class unpub. data). Thus, it seems highly probable that individuals in Las Caucheras can complete two life cycles within a year.

Some populations of tropical seabirds also complete life cycles of less than a year. For example, several years of study of sooty terns (*Sterna fuscata*) breeding on Ascension Island (7°57'S; 14°22'W; Chapin 1954) revealed that breeding and molting periods total to ~9.6 months. Therefore, molt and breeding occurs in all portions of the calendar year in *S. fuscata* (Chapin 1954; Ashmole 1963). Endogenous timing mechanisms, physiological constraints relating to molt and social cues may be important in the timing of *S. fuscata* life cycles, though the ultimate determinant of sooty tern life cycle timing is unclear (Chapin 1954; Chapin & Wing 1959; Ashmole 1963). In sum, studies of *Z. capensis* in Colombia and *S. fuscata* on Ascension Island demonstrate that in some tropical environments with low amplitude seasonality, or where large portions of the calendar year are suitable for breeding and molt, life cycles can simply be the sum of how long it takes to complete breeding, molting and/ or non-breeding periods and do not necessarily correspond to a 12 month cycle (Chapin 1954, Chapin & Wing 1959; Ashmole 1963). This is may also be the case in Las Caucheras, where – similar to *S. fuscata* on Ascension

Island – internal physiological rhythms as well as social synchronizing cues may important in determining life cycle of pairs.

Mechanisms for timing life history stages in *Z. capensis*

No single explanation for the timing of life history stages has been convincingly demonstrated for *Z. capensis*, but several mechanisms have been proposed. Photoperiod change is one possible mechanism for timing life history stages in some *Z. capensis* populations (Lewis et al. 1974). Photoperiod change is minimal in most tropical latitudes, however natural photoperiod changes can be perceived in at least some low-latitude species (spotted antbird, *Hylophylax navoides*, Hau et al. 1998). Moreover, previous experiments have shown *Z. capensis* respond to increasing photoperiod by becoming photostimulated (upregulating reproductive physiology and behavior), even in photoperiods equivalent to those at low latitudes (Epple et al. 1972; Farner & Lewis 1971; King 1973; Miller 1965). In one study on subtropical *Z. capensis* from Tucumán, Argentina (26°9'S; 65°13'W), increasing photoperiod stimulated reproductive physiology (as it was suspected to do in the wild), but did not appear to lead to a photorefractory phase, a period marked by the termination of physiological and behavioral responsiveness to long days that permits a physiological stop of reproduction, in birds exposed to either short or long photoperiods in over a year (Lewis et al. 1974). *Zonotrichia capensis* may therefore lack an absolute photorefractory phase (Lewis et al. 1974) or have a very short and/or flexible refractory phase (King 1973; Moore et al. 2006; Hahn & MacDougall-Shackleton 2008).

The photorefractory state is considered to be advantageous in that it allows species (including *Zonotrichia* breeding in the temperate-zone) to avoid or terminate reproduction during periods unsuitable for reproduction, and often marks the physiological transition to molt and/ or migration (Farner & Mewaldt 1955; Harris & Turek 1982; Farner et al. 1983). *Zonotrichia capensis* is phylogenetically basal to its temperate-zone congeners (Zink 1982; Zink et al. 1991; Zink & Blackwell 1996), thus the most parsimonious explanation for a lack of refractoriness is that it was secondarily lost (instead of independently derived in the other *Zonotrichia* species) as an adaptive specialization to low amplitude seasonality (Lewis et al. 1974; Hahn & MacDougall-Shackleton 2008). In this scenario, the cost of missing potential reproductive opportunities may be higher than the benefit of inhibiting reproduction during a portion of the year, even if it is slightly less seasonally favorable for breeding (Hahn & MacDougall-Shackleton 2008). However,

in some populations, like Las Caucheras, there may not be periods of the year that are consistently less (or more) favorable for reproduction.

Nevertheless, Lewis et al. (1974), similar to King (1973), found that *Z. capensis* showed a spontaneous collapse of gonadal tissue in a wild population, suggesting that they were incapable of breeding at that time (i.e., refractory). Given that a refractory period was observed in the wild, but not in Lewis's experimental population, the regression of gonadal tissue may not be absolute and/ or may not be exclusively controlled by photoperiod (Lewis et al 1974). Instead it seems likely that *Z. capensis* is relatively refractory, where reproductive physiology and behavior are down-regulated, but the cue response system remains flexibly responsive to cues predicting favorable times to breed (Farner et al. 1983; MacDougall-Shackleton & Hahn 2007; Hahn & MacDougall-Shackleton 2008). Though some studies demonstrate that low critical photoperiods (10-12 hrs light per day; Miller 1965; Lewis et al. 1974; Epple 1972) can photostimulate *Z. capensis*, no study has examined 1) what the critical day length needed to photostimulate *Z. capensis* in Las Caucheras is and 2) whether individuals in Las Caucheras are photostimulated year-round (which would be the case if 12 hours of light marked the critical day length needed for photostimulation). Just as in *Zonotrichia* existing in temperate-latitudes, the refractory period of subtropical and/ or tropical *Zonotrichia* could represent a brief – but important – period of physiological evaluation and recovery that marks the transition into another life cycle. In sum, refractory periods could be determined by photoperiod in some populations; however, in environments with near-equatorial photoperiod and low amplitude seasonality, individual physiological condition and social cues within each pair may be the most important determinants of refractory periods.

Environmental cues other than photoperiod have been proposed as primary timing mechanisms in seasonal populations existing in lower latitudes. In both Costa Rican (10°10'N 84°15'W; Wolf 1969) and Panamanian (8°50'N, 82°60'W; Kalma 1970) populations, the timing of reproduction was suggested to be primarily related to seasonal rainfall. Periods of super-rainy and rainy seasons, could predict shifts to high primary productivity and food availability, when breeding would be advantageous, with dryer periods corresponding to molt (Wolf 1969; Kalma 1970). In Perú (12° 30'S, 76°80'W), rainfall was ruled out as a proximate cue because the *Z. capensis* were inhabiting highly irrigated agricultural lands where water was always available, though seasonal sunshine and insect food were suggested as cues used to time seasonal breeding

and molt. It is important to note that photoperiod could influence seasonality in these populations, as it is known to influence populations at similar or lower latitudes (Hau et al 1998). However, more than one breeding period can occur per year and the timing of seasons is not highly precise, thus photoperiodic change is unlikely to be the primary cue for timing life history stages in Costa Rica, Panama and Peruvian populations (Wolf 1969, Kalma 1970; Davis 1971; Epple 1972; Lewis et al. 1974).

Populations of *Z. capensis* in Papallacta (0° 21'S, 78°09'W; 3300 m), Pintag (0° 22'S, 78°23'W; 2900 m), and Las Caucheras (0°37'S, 77°55' W; 2100 m), are all in close proximity to the equator, but all display unique seasonal (or aseasonal) life cycles. As in Papallacta (Bendix & Rafiqpoor 2001), photoperiod probably varies minimally in all three populations, thus it is unlikely that daily photoperiod change is a primary cue for the timing of life history stages (Moore per. comm.). Papallacta and Pintag show opposed breeding and molting periods, potentially related to seasonal precipitation, food availability, and/ or social synchronizing cues. This is hypothesized because though the two populations are only geographically separated by 25 km, their opposed seasonal rainfall regimes are determined by being on either side of the Andean divide (~4000 m), which creates a rain shadow and a formidable barrier to dispersal (Moore et al. 2005). Las Caucheras, on the other hand, is located at a lower altitude, receives heavy precipitation year-round, and individuals are not seasonally synchronized (Chapter II, V). While external cues may predict individual cycles, it seems more plausible that endogenous mechanisms limited by physiological state and constrained by receptive social signals, may ultimately determine life cycles in Las Caucheras. Thus, individuals in each population experience population-specific cycles in photoperiod, rainfall, temperature, and food availability and therefore may rely on different environmental variable(s) as cues depending on which variable(s) provide the most meaningful prediction of seasonal cycles influencing future reproduction. In populations where there is low amplitude of seasonality in environmental cues, it seems that social synchronizing cues may be the most critical for the timing life history stages at the level of each pair.

Molt and fitness trade-offs in the timing of life history stages

Molting of plumage restores degraded, broken and ineffective feathers, a process which is essential for survival (Dawson 2000; Dawson 2008; Rohwer et al. 2009). Feather quality can

communicate individual quality to potential mates (McGlothlin et al. 2007; Butler et al. 2008; de la Hera et al. 2009). Good quality plumage also permits efficient flight and effective thermoregulation (Nilsson & Svensson 1996; Schieltz & Murphy 1997; Butler et al. 2008; Cyr et al. 2008; Rohwer et al. 2009). Molting, like breeding, demands adequate food resources, benign climate and ample time (Murphy & King 1992; Dawson et al. 2000; Ricklefs & Wikelski 2002; Rohwer et al. 2009). Therefore, in seasonal species the temporal overlap of breeding and molt is often minimized, though there is selective pressure to maximize the time spent in each life history stage within favorable seasonal periods (Newton 1966; Wingfield & Farner 1978b; Murphy & King 1992). The timing of reproduction in seasonally breeding birds typically limits when molt can occur (Wingfield & Farner 1978a; Bauchinger & Klaassen 2005). However, diverse patterns of molt have evolved as adaptations to different environments and physiological constraints (Dawson et al. 2000; Pulido & Coppack 2004; Barta et al. 2008; Dawson 2008). For instance, molt strategies are diverse in migratory birds and may include either one or two complete molt cycles per year (Barta et al. 2008; Dawson 2008). Individual trade-offs of investment in reproduction versus self-maintenance via molt will therefore occur in every life cycle (Wingfield & Farner 1978a; Bauchinger & Klaassen 2005; Cooper et al. 2005; Weggler 2006).

In aseasonally breeding populations, molt remains a critical life history stage. However, the temporal calendar for breeding and molt is not related to a single overarching environmental cue, so individual physiology and/ or social cues within a pair of birds may be important in determining molt. In tropical seabirds that can breed year-round, molt also occurs year-round (Chapin 1954; Stonehouse 1962; Ashmole 1963; Snow 1965). In some populations with high competition for nest sites, breeding may ultimately take precedence over molt, leading to interrupted molt that is continued after breeding (Stonehouse 1962; Ashmole 1963; Schreiber & Ashmole 1970). Where breeding was synchronized, but not seasonal (could occur at any time of year), Chapin (1954) suggested that molt was equally important as breeding in timing life cycles in *S. fuscata*, because life cycles appeared to be the sum of molt and breeding. Thus, the physiological need to molt and the duration of individual molt in aseasonally breeding bird species may influence when breeding will occur (as well as visa versa) (Chapin 1954). In other aseasonal species, complexities related to a highly stochastic environment and low reproductive

success may select for high responsiveness to breeding and flexible scheduling of molt (Stonehouse 1962; Snow 1965).

Miller (1961, 1962) suggested that the timing of breeding in Colombian *Z. capensis* could be ultimately constrained by the physiological need to molt. The Colombian population of *Z. capensis* studied by Miller inhabited an environment characterized by high seasonal rainfall (that covered more than 8 months of the year in two seasons), and tall, thick grasses. Miller hypothesized that these environmental characteristics caused substantial feather wear (Miller 1961, 1962; Miller & Miller 1968). Further, the high ultraviolet light levels experienced by many tropical resident birds causes considerable feather damage (Nebel et al. 2002; Butler et al. 2008). In these circumstances there may be the need for two complete molts per year. Thus, the biannual life cycle proposed by Miller may depend as much on the timing and success of breeding as molt (Miller 1961).

The environment inhabited by Colombian *Z. capensis* is very similar to that of *Z. capensis* in Las Caucheras, except that Las Caucheras is even less seasonal, as rainfall is always high (Chapter V). In Las Caucheras, many *Z. capensis* were captured with damaged, highly worn and broken feathers in different periods of the year (Class unpub. obs.). Excessive plumage wear could relate to the high year-round precipitation, thick grassy habitat and high UV radiation at 2100 m in this humid, equatorial environment, similar to the Colombian population (Miller & Miller 1968; Nebel et al. 2002; Butler et al. 2008). Thus, frequent replacement of plumage may greatly improve thermoregulation, individual condition and flight efficiency in these conditions, leading to greater individual fitness. The success of breeding periods may depend (at least in part) on the quality of plumage.

In some populations of more seasonal *Z. capensis* a partial molt immediately precedes breeding (Davis 1971; King 1973). Davis (1971) believed that the partial molt he observed was actually the start of a second complete molt, because the molt pattern mirrored the molt sequence described in a study of complete molt of *Z. capensis* (Miller 1961). Davis hypothesized that this molt pattern was related to the seasonality of the environment (Davis 1971). However, Davis (1971) also predicted that such molts were critical to the success of subsequent breeding periods because a period of non-breeding typically preceded molts and because he noted substantial feather wear could result in negative fitness consequences.

Molt in food supplemented pairs of Z. capensis

The majority of food supplemented pairs of *Z. capensis* in both non-breeding and feeding fledglings life history stages initiated molt in response to augmented food supply (Chapter IV). The results of supplementation in Las Caucheras suggested that molt, rather than breeding, was the most advantageous life history stage in which experimental birds could invest excess food resources at the time they were supplemented. However, the result that birds molted after supplementation do not agree with previous studies that have provided food supplements and found birds advance the initiation of breeding (Schoech & Hahn 2007; 2008). Further, only one previous food supplementation study was conducted on a tropical species, the African stonechat, *Saxicola torquata*, which is highly seasonal (Scheuerlein & Gwinner 2002). We do not yet know if food supplementation studies in populations of birds existing in environments with low seasonality will show results similar to Las Caucheras.

The results of food supplementation in Las Caucheras were intriguing because they imply that 1) in supplemented pairs that were feeding fledglings, molting was more important to individual fitness than prolonging breeding (by investing in another brood) and 2) supplemented non-breeding pairs may have recently reproduced, but may be in a refractory period (of varying lengths), or that they may have molted prior to the non-breeding life history stage, but still responded to supplemental food by molting prior to breeding again. Molting typically follows breeding in *Z. capensis*, as in most other species (Dawson 2008). It therefore seems reasonable, that birds that had just finished breeding could use extra resources towards speeding the transition into molt (thus potentially speeding the transition into breeding again). In this respect, the results do not contradict previous studies that have examined the effect of food supplementation, but suggest that both seasonality and the timing of when supplements are provided (e.g., during the transition from molt to breeding or breeding to molt) may influence the response of tropical *Z. capensis* in Las Caucheras. Supplementation in pairs feeding fledglings therefore potentially led to some overlap of molting and feeding fledglings, as fledglings are estimated to reach complete independence of adults anywhere from 33-54 days (Miller & Miller 1968; Wolf 1969; Kalma 1970; King 1973).

Individual birds in Las Caucheras can be found in non-breeding condition after they finish breeding or molting (Class unpub. data). Therefore individuals in the non-breeding stage could be either transitioning from molt to breeding or from breeding to molt. From this

perspective, non-breeding periods may simply represent a pause prior to investment in the subsequent expensive life history stage. Furthermore, different individuals may spend different amounts of time in these pauses depending on individual physiological condition and stochastic events.

Food supplemented pairs that were feeding fledglings rapidly transitioned from breeding to molt, while control pairs that were feeding fledglings predominately entered non-breeding, strongly suggesting that food availability allowed supplemented birds to avoid the non-breeding pause between breeding and molting. Explaining the results of our non-breeding experiment is more complicated. It may be more selectively advantageous to breed immediately following molt – when feather quality is high - than to molt immediately following breeding. Therefore, I hypothesize that the transition from breeding to molt may last longer than the transition from molt to breeding. If true, this suggests that the majority of non-breeding birds are transitioning between breeding and molt, explaining why they molted in response to food supplementation. An alternate possibility is that non-breeding birds may undergo a partial molt prior to breeding, as documented in *Z. capensis* in Perú and Costa Rica (Wolf 1969, Davis 1971). This could occur because post-breeding molts may have been of poor quality or enough time has passed after a post-breeding molt that feathers have again become degraded. In both supplemental experiments, birds gained significant amounts of weight and fat scores were high when they were recaptured in molt (Chapter IV). Natural food resources are not usually enough to cause an increase in fat in Las Caucheras, so perhaps normal molts are generally poor quality and are not of comparable quality to the pre-migratory molt (which occurs in a period of abundant resources) of temperate congeners.

Constraints on timing life history stages within monogamous pairs

Interestingly, several studies have observed that male *Z. capensis* may have more physiological flexibility than females, especially in trade-offs related to breeding and molt (Miller 1965; Miller & Miller 1968; Davis 1971; Lewis et al. 1971; King 1973). Female *Z. capensis* only rarely interrupted molt in a study by Davis (1971). In many populations males also appear to have periods of prolonged receptivity, sometimes overlapping with molt (Miller & Miller 1968; Davis 1971; King 1973; Lewis et al. 1974). Further, females appeared to down-regulate reproductive physiology completely on experimental photoperiod regimes, while males

maintained reproductive physiology (Miller 1965). Females also typically provide the majority of parental care, as observed in Colombia (Miller & Miller 1968) and the Las Caucheras population (Chapter III). Therefore, females may face higher energetic and physiological costs than males during reproduction and afterward. Given that females incur more costs during reproduction, it seems likely that the rate of female molt may constrain the timing of reproduction, and receptive cues provided by females will determine when males can breed. Feather wear, particularly during breeding may also select for a complete molt prior to the subsequent breeding period in Las Caucheras females. Females may therefore ultimately determine the timing of reproduction through social cues (receptivity) towards the male, in spite of the fact that the male may be capable of breeding in much longer periods.

Future directions

Experiments that follow individuals through seasons over the course of several years can help reveal the pattern in individual cycles in nature. For instance, reciprocal transplants of individuals from different *Z. capensis* populations at the same latitude would reveal any genetic basis to cue recognition and timing systems. It also remains unclear how endogenous rhythms affect timing in *Z. capensis* in Las Caucheras, where environmental seasonality is low and no major cues are currently apparent. Controlled aviary experiments to test how endogenous rhythms may influence life cycle timing and whether one sex can influence the timing of another would help clarify such relationships. Experiments might also test the precise daily light needed to photostimulate *Z. capensis* at distinct latitudes and habitats to determine flexibility in cue perception. Investigations determining the mechanism affecting population asynchrony also seem critical to determining why pairs of *Z. capensis* in *Las Caucheras* are asynchronous. A first step may be to examine whether there are periods of slightly higher food resources and predation over several years. Experiments investigating trade-offs among the sexes, reproductive benefit of providing care and energetic cost of molt could also increase our understanding of how each sex influences reproductive behavior.

Conclusion

Different populations of aseasonal birds appear to use a diversity of life history strategies and time reproduction and molt according to specific constraints in their environment. *Zonotrichia*

capensis shows marked diversity in the timing of life cycles across its range and in which mechanism(s) are most useful in timing life history stages within life cycles. However, initial investigations (1950s - 1970s) of these questions in *Z. capensis* have not been revisited in the light of theoretical and technological advances. Thus, variation within *Zonotrichia* and even within *Z. capensis* is a rich resource that remains largely open to investigations of the evolution and flexibility of cue response systems in distinct habitats.

Literature Cited

- Ashmole, N. P. 1963 The regulation of numbers of tropical oceanic birds. *Ibis* **103b**, 297-364.
- Baker, J. R., Marshall, A. J. & Harrison, T. H. 1940 The seasons in a tropical rain-forest (New Hebrides). Part 5. Birds (*Pachycephala*). *Journal of the Linnean Society of Zoology*.
- Barta, Z., McNamara, J. M., Houston, A. I., Weber, T. P., Hedenstrom, A. & Fero, O. 2008 Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 211-229.
- Bauchinger, U. & Klaassen, M. 2005 Longer days in spring than in autumn accelerate migration speed of passerine birds. *Journal of Avian Biology* **36**, 3-5.
- Bendix, J. & Rafiqpoor, M. D. 2001 Studies on the thermal conditions of soils at the upper tree line in the paramo of Papallacta (eastern cordillera of Ecuador). *Erdkunde* **55**, 257-276.
- Boag, P. T. & Grant, P. R. 1984 Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecological Monographs* **54**, 463-489.
- Butler, L. K., Rohwer, S. & Speidel, M. G. 2008 Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *Journal of Avian Biology* **39**, 629-639.
- Chapin, J. P. 1954 The calendar of wideawake fair. *Auk* **71**, 1-15.
- Chapin, J. P. & Wing, L. W. 1959 The wideawake calendar, 1953-1958. *Auk* **76**, 153-158.
- Cooper, C. B., Hochachka, W. M., Butcher, G. & Dhondt, A. A. 2005 Seasonal and latitudinal trends in clutch size: Thermal constraints during laying and incubation. *Ecology* **86**, 2018-2031.
- Cyr, N. E., Wikelski, M. & Romero, L. M. 2008 Increased energy expenditure but decreased stress responsiveness during molt. *Physiological and Biochemical Zoology* **81**, 452-462.

- Davis, J. 1971 Breeding and molt schedules of the rufous-collared sparrow in coastal Peru. *The Condor* **73**, 127-146.
- Dawson, A. 2008 Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 1621-1633.
- Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C. & Eccleston, L. 2000 Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society B* **267**, 2093-2098.
- Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. 2001 Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* **16**, 365-380.
- de la Hera, I., Perez-Tris, J. & Telleria, J. L. 2009 Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biological Journal of the Linnean Society* **97**, 98-105.
- Diamond, A. W. 1975 Biology and behavior of frigatebirds (*fregata* spp.) on Aldabra Atoll. *Ibis* **117**, 302-323.
- Epple, A., Orians, G. H., Farner, D. S. & Lewis, R. A. 1972 The photoperiodic resticular response of a tropical finch, *Zonotrichia capensis costaricensis*. *The Condor* **74**, 1-4.
- Farner, D. S., Donham, R. S., Matt, K. S., Mattocks, J., P.W., Moore, M. C. & Wingfield, J. C. 1983 The nature of photorefractoriness. In *Avian endocrinology: environmental and ecological perspectives* (ed. K. H. S.I. Mikami, M. Wada), pp. 149-156. Tokyo, Japan; Berlin, Germany: Japan Scientific Society Press; Springer.
- Farner, D. S. & Lewis, R. A. 1971 Photoperiodism and reproductive cycles in birds. *Photophysiology* **6**, 325-370.
- Farner, D. S. & Mewaldt, L. R. 1955 The natural termination of the refractory period in the white-crowned sparrow. *Condor* **57**, 112-116.
- Follett, B. K. & Nicholls, T. J. 1984 Photorefractoriness in Japanese quail: possible involvement of the thyroid gland. *Journal of Experimental Zoology* **232**, 573-580.
- Gwinner, E. 1996 Circannual clocks in avian reproduction and migration. *Ibis* **138**, 47-63.
- Gwinner, E. 2003 Circannual rhythms in birds. *Current Opinion in Neurobiology* **13**, 770-778.

- Hahn, T. P. & MacDougall-Shackleton, S. A. 2008 Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 267-286.
- Harris, M. O. & Turek, F. W. 1982 Photoperiodic control of the timing of testicular regression in white-throated sparrows. *General and Comparative Endocrinology* **46**, 124-129.
- Harris, M. P. 1969 Factors influencing the breeding cycle of the red-billed tropicbird in the Galapagos Islands. *Ardea* **57**, 149-157.
- Hau, M. 2001 Timing of breeding in variable environments: Tropical birds as model systems. *Hormones and Behavior* **40**, 281-290.
- Hau, M., Perfito, N. & Moore, I. T. 2008 Timing of breeding in tropical birds: Mechanisms and evolutionary implications. *Ornitologia Neotropical* **19 (Suppl.)**, 39-59.
- Hau, M., Wikelski, M., Gwinner, H. & Gwinner, E. 2004 Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* **106**, 489-500.
- Hau, M., Wikelski, M. & Wingfield, J. C. 1998 A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 89-95.
- Jacobs, J. D. & Wingfield, J. C. 2000 Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* **102**, 35-51.
- Kalma, D. L. 1970 Some aspects of the breeding ecology and annual cycle of three populations of the rufous-collared sparrow (*Zonotrichia capensis*) in Western Panama, pp. 218. New Haven: Yale.
- King, J. R. 1973 The annual cycle of the rufous-collared sparrow (*Zonotrichia capensis*) in three biotopes in northwestern Argentina. *Journal of Zoology, London* **170**, 163-188.
- Lewis, R. A., King, J. R. & Farner, D. S. 1974 Photoperiodic responses of a subtropical population of finch (*Zonotrichia capensis hypoleuca*). *Condor* **76**, 233-237.
- Lofts, B. & Murton, R. K. 1968 Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *Journal of Zoology, London* **155**, 327-394.
- MacDougall-Shackleton, S. A. & Hahn, T. P. 2007 Adaptation and evolution of photoperiod response systems in birds. *Journal of Ornithology* **148**, S219-S224.

- McGlothlin, J. W., Duffy, D. L., Henry-Freeman, J. L. & Ketterson, E. D. 2007 Diet quality affects an attractive white plumage pattern in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology* **61**, 1391-1399.
- Miller, A. H. 1961 Molt cycles in equatorial Andean sparrows. *The Condor* **63**, 143-161.
- Miller, A. H. 1962 Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **48**, 396-400.
- Miller, A. H. 1965 Capacity for photoperiodic response and endogenous factors in the reproductive cycles of an equatorial sparrow. *Proceedings of the National Academy of Sciences, USA* **54**, 97-101.
- Miller, A. H. & Miller, V. D. 1968 The behavioral ecology and breeding biology of the Andean sparrow, *Zonotrichia capensis*. *Caldasia* **10**, 83-154.
- Moore, I. T., Bentley, G. E., Wotus, C. & Wingfield, J. C. 2006 Photoperiod-independent changes in immunoreactive brain gonadotropin-releasing hormone (GnRH) in a free-living, tropical bird. *Brain Behavior and Evolution* **68**, 37-44.
- Moore, I. T., Bonier, F. & Wingfield, J. C. 2005 Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology* **16**, 755-762.
- Moore, I. T., Wada, H., Perfito, N., Busch, D. S. & Wingfield, J. C. 2004 Territoriality and testosterone in an equatorial population of rufous-collared sparrows, *Zonotrichia capensis*. *Animal Behaviour* **67**, 411-420.
- Moreau, R. E., Wilk, A. L. & Rowan, W. 1947 The moult and gonad cycles of three species of birds at five degrees south of the equator. *Proceedings of the Zoological Society* **117**, 345-364.
- Murphy, M. E. & King, J. R. 1992 Energy and nutrient use during molt by white-crowned sparrows *Zonotrichia leucophrys glambelii*. *Ornis Scandinavica* **23**, 304-313.
- Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford, U. K.: Clarendon Press.
- Nebel, S., Lank, D. B., O'Hara, P. D., Fernandez, G., Haase, B., Delgado, F., Estela, F. A., Ogden, L. J. E., Harrington, B., Kus, B. E., Lyons, J. E., Mercier, F., Ortego, B., Takekawa, J. Y., Warnock, N. & Warnock, S. E. 2002 Western sandpipers (*Calidris mauri*) during the nonbreeding season: Spatial segregation on a hemispheric scale. *Auk* **119**, 922-928.
- Newton, I. 1966 The moult of the bullfinch *Pyrrhula pyrrhula*. *Ibis* **108**, 41-67.

- Nicholls, T. J., Goldsmith, A. R. & Dawson, A. 1988 Photorefractoriness in birds and comparison with mammals. *Physiological Reviews* **68**, 133-176.
- Nilsson, J. A. & Svensson, E. 1996 The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**, 711-714.
- Perfito, N., Kwong, J. M. Y., Bentley, G. E. & Hau, M. 2008 Cue hierarchies and testicular development: Is food a more potent stimulus than day length in an opportunistic breeder (*Taeniopygia g. guttata*)? *Hormones and Behavior* **53**, 567-572.
- Pulido, F. & Coppack, T. 2004 Correlation between timing of juvenile moult and onset of migration in the blackcap, *Sylvia atricapilla*. *Animal Behaviour* **68**, 167-173.
- Ricklefs, R. E. & Wikelski, M. 2002 The physiology/life-history nexus. *Trends in Ecology & Evolution* **17**, 462-468.
- Rohwer, S., Ricklefs, R. E., Rohwer, V. G. & Copple, M. M. 2009 Allometry of the duration of flight feather molt in birds. *PLoS Biol* **7**, e1000132.
- Scheuerlein, A. & Gwinner, E. 2002 Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. *Journal of Biological Rhythms* **17**, 171-180.
- Schieltz, P. C. & Murphy, M. E. 1997 The contribution of insulation changes to the energy cost of avian molt. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **75**, 396-400.
- Schoech, S. J. & Hahn, T. P. 2007 Food supplementation and timing of reproduction: does the responsiveness to supplementary information vary with latitude? *Journal of Ornithology* **148**, S625-S632.
- Schoech, S. J. & Hahn, T. P. 2008 Latitude affects degree of advancement in laying by birds in response to food supplementation: a meta-analysis. *Oecologia* **157**, 369-376.
- Schreiber, R. W. & Ashmole, P. N. 1970 Sea-bird breeding seasons on Christmas island, Pacific Ocean. *Ibis* **112**, 363-394.
- Small, T. W. & Moore, I. T. 2009 Seasonal neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding birds. *General and Comparative Endocrinology* **163**, 135-141.

- Snow, D. W. 1965 The breeding of the red-billed tropic bird in the Galapagos Islands. *The Condor* **67**, 210-214.
- Stonehouse, B. 1962 The tropicbirds (genus *Phaethon*) of Ascension Island. *Ibis* **103B**, 124-161.
- Strand, C. R., Small, T. W. & Deviche, P. 2007 Plasticity of the Rufous-winged Sparrow, *Aimophila carpalis*, song control regions during the monsoon-associated summer breeding period. *Hormones and Behavior* **52**, 401-408.
- Stutchbury, B. J. M. & Morton, E. S. 2001 *Behavioral Ecology of Tropical Birds*. San Diego: Academic Press.
- Stutchbury, B. J. M. & Morton, E. S. 2008 Recent advances in the behavioral ecology of tropical birds - The 2005 Margaret Morse Nice Lecture. *Wilson Journal of Ornithology* **120**, 26-37.
- Wegglar, M. 2006 Constraints on, and determinants of, the annual number of breeding attempts in the multi-brooded Black Redstart, *Phoenicurus ochruros*. *Ibis* **148**, 273-284.
- Wikelski, M., Martin, L. B., Scheuerlein, A., Robinson, M. T., Robinson, N. D., Heim, B., Hau, M. & Gwinner, E. 2008 Avian circannual clocks: adaptive significance and possible involvement of energy turnover in their proximate control. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 411-423.
- Wingfield, J. C. & Farner, D. S. 1978a The annual cycle of plasma irLH and steroid hormones in feral populations of the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biology of Reproduction* **19**, 1046-1056.
- Wingfield, J. C. & Farner, D. S. 1978b The endocrinology of a natural breeding population of the white-crowned sparrow (*Zonotrichia leucophrys pugetensis*). *Physiological Zoology* **51**, 188-205.
- Wingfield, J. C., Hahn, T. P., Levin, R. & Honey, P. 1992 Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology* **261**, 214-231.
- Wolf, L. L. 1969 Breeding and molting periods in a Costa Rican population of the Andean sparrow. *The Condor* **71**, 212-219.
- Zink R. M. 1982 Patterns of genic and morphological variation among sparrows in the genera *Zonotrichia*, *Melospiza*, *Junco* and *Passerella*. *Auk* **99**, 632-649.
- Zink, R. M. & Blackwell, R. C. 1996 Patterna of allozyme, mitochondrial DNA, and morphometric variation in four sparrow genera. *Auk* **113**, 59-67.

Zink, R. M., Dittman, D. L. & Rootes, W. L. 1991 Mitochondrial DNA variation and the phylogeny of *Zonotrichia*. *Auk* **108**, 578-584.