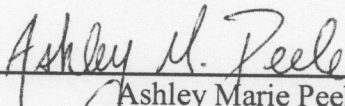


POPULATION REGULATION OF A MIGRATORY SONGBIRD IN THE
NON-BREEDING SEASON: A TEST OF BUFFER AND CROWDING
EFFECTS

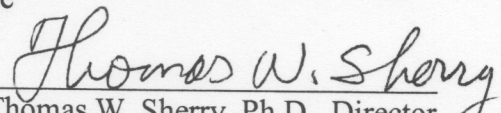
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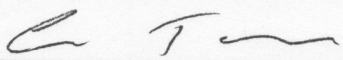
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TO THE DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
OF THE SCHOOL OF SCIENCE AND ENGINEERING
OF TULANE UNIVERSITY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

BY

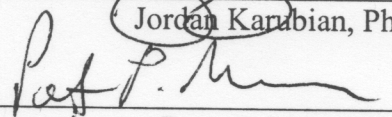

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ABSTRACT

Animal populations are limited by their environment and interactions with one another, the latter proportional to density. How density-dependent mechanisms regulate populations is poorly understood, particularly for migratory animals. Winter, or non-breeding, mechanisms remain particularly poorly understood for almost all migratory bird species. This dissertation tested the hypothesis that American Redstarts (*Setophaga ruticilla*) are regulated both within and between habitats in the winter by two mechanisms, a crowding effect and a buffer effect. As population size increases, crowding increases competition for space and resources and more individuals are relegated to lower quality habitats and forced into a transient behavioral strategy, which buffers high quality habitats from negative feedback of density. My study was carried out in Jamaica, where redstarts occupy diverse habitats. I found that population size varied among habitats, but accounting for both territorial and transient individuals was critical for accurate assessment of this variation. Ecological conditions drive differences in habitat suitability and redstart density at multiple spatial scales. Regionally, redstart survival, density, and numbers of transient individuals distinguish inland from coastal populations, consistent with differences in ecological conditions (e.g. rainfall). Locally, timing of spring departure, as well as age and sex structure distinguish neighboring habitats, consistent with increased competition for food. When population size increased over the years of this study, changes in local density were similar among habitats, and thus not the result of a buffer effect. However, increasing densities decreased food

availability, which corresponded with negative feedback on departure timing and territorial behavior, i.e. more transients, in poorer habitats. This supported a crowding effect on spatial behavior (territoriality) and late-winter condition of individuals relegated to low suitability habitats. High quality inland habitats appear to buffer individuals from the effects of changing population abundance, as well as ecological conditions, evidence of a regional buffer effect.

POPULATION REGULATION OF A MIGRATORY SONGBIRD IN THE
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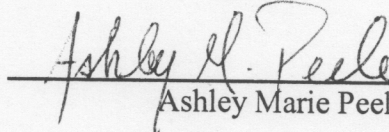
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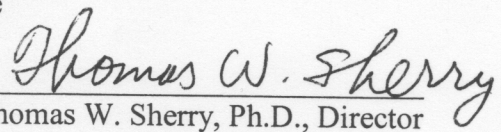
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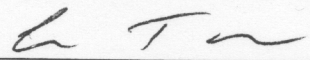
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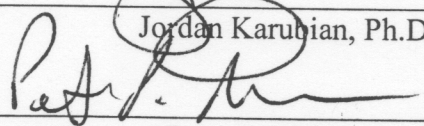

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Chapter 1

Mechanisms of change in migratory populations

Regulation and limitation in bird populations: Introduction

Population abundance is affected by both ecological factors independent of population size and by density-dependent feedback that regulates the population to a limited range of abundances. Density-independent mechanisms can limit animal populations through changes in habitat availability or quality, e.g., via climate (Nevoux et al. 2008, Pearce-Higgins et al. 2009, Both et al. 2010). Climate effects, typically too much or too little precipitation, can impact food resources negatively, thereby reducing habitat quality (Strong and Sherry 2000, Ockendon et al. 2014a). Concurrently, density-dependent feedbacks on reproduction and survival are known from diverse taxa, including birds (Mallord et al. 2007, Brouwer et al. 2009, Ashbrook et al. 2010), mammals (Becker et al. 2009), fish (Utz and Hartman 2009, Lobón-Cerviá 2010), plants (Morschauser et al. 2009, Treberg and Turkington 2010), and insects (Miller 2007).

Regulation can involve diverse mechanisms. One of the best-studied mechanisms is crowding, also known as neighborhood effects, involving negative feedback from close neighbors, e.g., via food competition, aggressive interactions, stress (Bradshaw et al. 2000, Wilson et al. 2006, Rotella et al. 2009, Marra et al. in review), or predation. Another mechanism of regulation is site-dependence, which occurs when preemptive site use by growing populations forces more individuals to occupy poorer quality territories

(Rodenhause et al. 1997) resulting in a decrease in average vital rates (Rodenhause et al. 2003, Nevoux et al. 2011, Ferrer et al. 2014). At a larger spatial scale (among habitats) the buffer effect mechanism operates across a gradient of habitats differing in quality, and results from larger populations forcing more individuals into worse habitats and into non-territorial (floater) or transient behavior via social interactions (e.g., territoriality; Kluver and Tinbergen 1953, Brown 1969). How density-dependent and independent mechanisms combine to shape annual fluctuations in population size is still unanswered in most species.

Understanding population limitation in birds, especially migratory birds, remains particularly challenging due to their often-prodigious movements. Many bird species breeding at temperate latitudes migrate to the tropics for the nonbreeding season, which exposes them to a wide range of ecological conditions throughout the annual cycle (Terborgh 1989, Newton 2004). Carryover effects between different stages of this cycle means that conditions encountered in any one period may limit populations in subsequent seasons (Webster et al. 2002, Runge and Marra 2005, Finch et al. 2014). Moreover, North American migrants declined beginning in the early 1960s (Robbins et al. 1989), and many species continue to decline, but we still don't understand what limits or regulates most of these populations (Newton 2004).

Circumstances on the breeding grounds have long been a focus of population-limiting and regulating factors in migratory birds, in part because of the relative ease of studying nesting ecology. For example, habitat quality of nest sites predicts reproductive success; thus the number of low-quality sites occupied is proportional to annual population density, indicating density-dependent population regulation (Rodenhause et

al. 2003, Kokko et al. 2004, Nevoux et al. 2011). However, evidence is accumulating that conditions during the migratory period and wintering season are equally important in population limitation and regulation (Faaborg and Holmes 2010).

Increasingly, research has shown that winter habitat quality defined by ecological conditions such as climate and food limits the survival of migratory birds (Wunderle 1995, Lefebvre and Poulin 1996, Marra and Holberton 1998, Strong and Sherry 2000, Latta and Faaborg 2001, Borgmann et al. 2004, Gunnarsson et al. 2005, Johnson et al. 2006, Wilson et al. 2011). Demographic responses to these ecological conditions mediate their impact on population abundance (Newton 2004) via density-dependent feedback or regulation (Brown 1969, Fretwell 1972). However, very few studies have assessed potential mechanisms of regulation in winter, non-breeding populations (but see Gill et al. 2001, Durell et al. 2004, Gunnarsson et al. 2005, Ntiamoa-Baidu et al. 2014, Marra et al. in review), and none has tested how these mechanisms may affect birds that overwinter in multiple habitats.

To understand winter limitation requires considering the entire annual cycle, because it is difficult to isolate one season from the next due to carryover effects. Most knowledge of carryover effects comes from studies of how winter conditions affect reproductive success (Norris et al. 2004, Reudink et al. 2009a, Duriez et al. 2012, Finch et al. 2014). These ecological constraints from the wintering season, such as food limitation (Strong et al. 2000), impact spring departure and arrival timing, and fecundity of migratory species (Norris et al. 2004, Reudink et al. 2009a, Ockendon et al. 2014b). This suggests that regulating effects on the wintering grounds could be delayed so as to impact breeding season performance and survival of migratory species (Gill et al. 2001,

Sillett et al. 2004), but we know little about how density-dependence in winter contributes to carry-over effects for most species of birds.

Several mechanisms of population regulation are applicable in the non-breeding season. Crowding effects occur as increasing population density limits food availability and increases competition among neighboring individuals (Lack 1954). In winter, this results in reduced body condition and lower survival (Marra et al. in review). As population size increases, a buffer effect can also force more individuals to occupy poorer wintering habitats, which reduces population survival rates and performance (Gill et al. 2001, Gunnarsson et al. 2005, Ntiamoa-Baidu et al. 2014). Site-dependence also recognizes individuals occupying increasingly poor quality sites—either territories or habitats—as population size increases (Rodenhouse et al. 1997), and thus makes similar predictions to the buffer effects hypothesis.

All of these mechanisms are driven by the interaction of bird demography with habitat suitability, and are not mutually exclusive. In territorial species, social dominance mechanisms often exclude subordinate individuals from higher quality territories or habitats in the non-breeding season (Marra 2000, Latta and Faaborg 2001). Thus, the buffer effect likely mediates a crowding effect via increased competition for resources by pushing subordinate individuals into poorer habitats. To understand the mechanism of a buffer effect, as opposed to pattern alone (Ntiamoa-Baidu 2014, Sullivan et al. 2015), one must also understand both within and among-habitat density-dependent effects. To date, no studies have looked at both large-scale (multiple habitats and regions; buffer effect) and local (crowding) mechanisms of population regulation in the same species during the non-breeding season.

Understanding how these mechanisms may impact species' responses to changing ecological conditions is critical for predicting the impact of global change on migratory populations. For example, tropical habitats are disappearing due to deforestation and urban expansion at rapid rates (Newbold et al. 2014, Newman et al. 2014). Global climate change also threatens tropical regions with prolonged drought (Neelin et al. 2006) and intensified El Niños (Silleet et al. 2000). Such changes will inevitably affect winter habitat quantity and quality, and the ability of tropical regions to support migratory populations. Identifying which habitats are most likely to shield populations against these challenges could better inform conservation management strategies.

To address these issues, I tested the hypothesis that a large-scale mechanism, the buffer effect, regulates population size of a migratory songbird among diverse winter habitats, while also assessing the effects of within-habitat changes in density over time. Quantifying abundance among structurally variable habitats in the non-breeding season can be challenging, so I first assessed and validated a method to quantify density of individuals with as little bias as possible. Next, I tested whether habitats varied in their relative suitability, based on ecological and population indicators of quality. Finally, I compared the affect of increasing population density on distribution and demography of individuals among habitats to test whether poorer sites buffered high quality habitats.

Organization and Scope of the Dissertation

Testing a buffer effect mechanism requires accurate estimates of density among diverse habitats. Thus in Chapter 2, I tested and validated a relatively new method for quantifying population size, distance-sampling surveys, compared to territory mapping using marked individuals. Comparison of densities derived from these methods revealed

distance-sampling estimates significantly higher than territory mapping in two of the study habitats (mangrove and scrub). This highlighted a critical but often overlooked component of estimating population abundance and density, which is accounting for the occurrence and number of individuals with alternative spatial behaviors, often referred to as “transients”. Comparison of annual capture records with territory maps showed that (1) proportionally more transient individuals were captured on mangrove and scrub sites relative to wet limestone and citrus, and (2) transient individuals differed from territorial individuals, tending to be socially subordinate classes of individuals, namely females and yearling males. These results provide evidence to explain some of the disparity between distance sampling and territory mapping density estimates, suggest social dominance relationships as a cause of transience, and demonstrate an unexpectedly high number of transient individuals in coastal redstart populations.

In Chapter 3, I tested for a suitability gradient among the available winter habitats, as the next step in assessing a buffer effect mechanism. Understanding how ecological conditions (food, rainfall) affect populations across a large spatial and temporal scale requires multiple indicators of habitat quality (Johnson 2007); thus I measured redstart annual survival, age and sex ratios, spring departure dates, and proportions of transients. I compared these suitability indicators among specific Jamaican habitat types, as well as regions (coastal vs. inland), because some ecological conditions (e.g. climate) vary more across larger spatial scales than locally. These results suggested that regional variation in ecological conditions affect annual survival and numbers of transients, while local conditions affect spring departure, age and sex structure. Redstart densities varied across both spatial scales. These results were surprising, and differed from past assessments of

quality among similar habitats (Johnson et al. 2006), which latter showed greater uniformity of indicators across habitats, but did not account for regional effects. Based on these results, habitat suitability is more complex than a simple linear gradient of quality, and important variation may be missed when studies are too limited spatially.

Based on the complex habitat gradients identified in Chapter 3, I assessed in Chapter 4 the pattern and impact of buffer effect mechanism between habitats, and the effects of density on within-habitat crowding effects, using both spatio-temporal abundance patterns and demographic characteristics of populations. An increasing total population size over the first three years of my study allowed me to test whether habitat-specific populations of redstarts responded differently to both changing population size and ecological conditions. I found that a buffer effect did not increase densities more in low quality habitats as population size increased. However, differences in survival, spring departure timing, and transience were consistent with changing density among regions and habitats, which suggested density-dependent feedback on individuals.

Demographic variation in redstart populations among all habitats studied suggested regulatory buffer effects at multiple spatial scales. Locally, increasing density corresponded to declining food availability, later departure date, and more transients particularly in poorer habitats, suggesting both a buffer and crowding effect. High quality inland wet limestone forest habitat experienced a comparable increase in density and a decline in food availability, but individuals occupying this habitat had earlier departure times and few transients were observed. Birds occupying wet limestone habitat appear to have been buffered against fluctuations in population size by relatively better ecological conditions, while low availability of resources in other habitats led to greater crowding

effects on spatial behavior and carryover effects.

Finally, in Chapter 5 I review overall findings and implications for regulation and conservation of migratory species. This study is the first to demonstrate that transients are a substantial component of a non-breeding population in Neotropical wintering habitats and that these birds are linked to density-dependent population dynamics. My findings raised more questions than they answered regarding the importance and effects of transients, but highlight the need for further research on movement and spatial patterns of migratory birds in winter. Additionally, I found that habitat quality gradients occur at multiple spatial scales in winter, revealing more complex interactions between ecological conditions and bird demography. Lastly, I showed for the first time that local crowding and a regional buffer effect regulate populations of a migratory songbird. This furthers our understanding of how a migratory species interacts with the complex variety of habitats and conditions encountered in winter, and informs conservationists on the importance of preserving the kinds of habitats, like tropical wet forests, that can best buffer wintering migrant populations against population declines.

Chapter 2

Combining survey methods to estimate abundance and transience of migratory birds among tropical non-breeding habitats.

ABSTRACT

Estimating population abundance in territorial species is challenging because individuals often differ behaviorally (e.g. transience, multi-territoriality), and thus in detectability. How well prevailing methods detect and quantify individuals using multiple strategies is rarely addressed. In our effort to quantify avian density and transience among diverse non-breeding habitats efficiently, we combined ‘unmarked’ (distance-sampling) with traditional ‘marked’ methods using a migratory passerine, the American Redstart (*Setophaga ruticilla*) wintering in three Jamaican habitats from 2010-2012. We predicted that the unmarked method would detect not only all known (marked) territorial individuals, but also individuals that were transient or non-territorial in these same habitats. Abundance estimates generated by our best unmarked model identified high proportions of transient individuals (up to 50%) occurring in two of these habitats, coastal dry scrub and mangrove, and virtually none in the third habitat, higher elevation wet limestone forest. Data derived from our marked method (systematic netting and banding plus territory mapping of color-marked individuals) confirmed the presence of these transient birds, and demonstrated that the unmarked method produced less biased estimates of the total abundance of redstarts in a given area, and did so more

efficiently than the marked method. However, the marked method was necessary for confirming the presence and identity of transient individuals. Documenting so many non-territorial individuals, disproportionately females and yearlings, in some habitat-year combinations indicates the need to determine what role these individuals play in population processes. Our results illustrate how unmarked and territory-mapping methods can be coupled to establish which individuals are either transient or floaters from neighboring areas. Combined, they provide a powerful tool for quantifying the range and variation of space-use strategies deployed by non-breeding individuals.

INTRODUCTION

Estimating the abundance of animal populations is fundamental to many ecological and conservation questions. Similarly, assessing population change over time requires single estimates of total abundance over repeated visits in time and space. Species with alternative reproductive or survival strategies typically contain multiple classes of individuals, such as territorial and transient, potentially differing in detectability and that must be included to estimate total population size (Brown and Long 2007, Penteriani et al. 2011, Segura et al. 2012). Most methods for quantifying mobile animals like birds take advantage of detecting territorial individuals, whose behaviors, singing and territory defense make them relatively easy to detect. Transient individuals partially or entirely abandon this strategy, defending no territory and moving more often and over greater distances than territorial individuals (Brown and Long 2007). As such, these individuals may be less vocal and more mobile, which can lead to lower detectability.

The question of bias in surveying and detecting such individuals via marked or unmarked methods is rarely explored (Pollock et al. 2002, Schmidt et al. 2013). This is an important issue for unbiased estimation of abundance, and in turn for understanding how patterns of distribution and abundance relate to environmental conditions or habitat. We do not know how transients, either temporary visitors to a site, with territories elsewhere, or non-territorial individuals within a survey interval, affect territorial individuals and broader demographic processes (Davies and Houston 1981, Brown and Long 2007). However, increases in the numbers of transient individuals in territorial species can reflect local or regional habitat loss and degradation, response to climate change, or increases in overall population size (Penteriani et al. 2005, Brown and Long 2007, Penteriani et al. 2011).

Transient behaviors have been documented in many Neotropical-Nearctic migratory birds (Winker et al. 1998, Brown and Long 2007, Brown and Sherry 2008, Lenda et al. 2012, Ruiz-Gutierrez et al. in review). Many of these species spend more than two-thirds of the annual cycle on non-breeding (hereafter winter) areas and in diverse habitats, and are thought to be primarily territorial on their wintering grounds (Greenberg and Salewski 2005, Salewski and Jones 2006). During winter, territoriality and dominance relationships can occur between and within species (e.g., Marra 2000, Toms 2013). Individuals within a population can exhibit a variety of behavioral responses as a consequence of dominance. For example, in species such as the American Redstart (*Setophaga ruticilla*), Black-throated Blue Warbler (*S. caerulescens*), and Prairie Warbler (*S. discolor*), social dominance hierarchies result in exclusion of subordinate individuals from preferred habitats (Marra et al. 1993, Wunderle 1995, Marra 2000, Latta and

Faaborg 2001). This leads some individuals to adopt alternative strategies including multiple territories, larger home ranges, or floater behaviors (Greenberg and Salewski 2005, Brown and Long 2007, Townsend et al. 2012, Toms 2013), which we label as ‘transient’ strategies for the purposes of this study. Birds may also adopt a transient strategy in low-resource years or habitats, when greater mobility allows better access to food sources over a larger area (Brown and Sherry 2008). Thus multiple mechanisms including the inherent mobility of birds as well as their social dominance structure may lead to transient behaviors. Survey methods that are less biased to the variety of behaviors exhibited by both transient and territorial individuals across multiple habitats are needed to better assess the presence and proportions of such individuals in the population.

Marked, survey methods, specifically territory mapping, are widely used for estimating the abundance of individuals in populations. Territory mapping – capturing, marking individuals, and mapping their space use and movements – has been used to estimate territorial density (territories per unit area) accurately (Wunderle 1995, Sillett et al. 2004, Johnson et al. 2006), providing an area abundance estimate. However, this method may have difficulty in identifying and counting individuals with alternative behavioral strategies, such as transients, particularly those that remain unmarked and thus unidentifiable as individuals (Brown and Long 2007). Lin et al. (2011) found that territory mapping was a less effective method of population abundance estimation than unmarked methods in the tropics, due to more movement (transient behaviors) of tropical resident forest species. Failure to detect transient individuals may bias population density estimates by underestimating total abundance.

Unmarked survey methods entail tallying all individuals detected during a given time interval. Several unmarked methods are routine, including multiple-observer (Garton and Kissling 2006), repeat-count (Kéry et al. 2005, Dail and Madsen 2011), removal methods (Farnsworth et al. 2002, Reidy et al. 2011, Chandler and King 2011), and distance sampling (Buckland et al. 2001). Relatively unbiased estimates of abundance have been possible with multiple methods, typically distance sampling (estimating distance of birds from observer) done simultaneously with repeat-counts, facilitating greater probability of detection and thus accuracy (Buckland et al. 2001, Farnsworth et al. 2001, Gale et al. 2009, Sillett et al. 2012). Many or most detections are typically made from call or song cues. Unmarked methods generally are more efficient at estimating abundance of all individuals, territorial and transient alike, but are limited in their capacity to quantify age, sex, and physiological or territorial status, i.e., entities critical to population processes.

Current methods for identifying and estimating transient individuals are limited to radio tracking, estimating movements via capture-mark-recapture (CMR) models (Pradel et al. 1997, Hines et al. 2003) or multi-state models to infer movement (Oro et al. 2004, Henaux et al. 2007, Schaub and von Hirschheydt 2009). Radio tracking remains expensive, time-intensive, and typically results in small sample sizes. CMR or multi-state models also require significant time and resources, and are typically used to estimate demographic parameters such as probability of survival or breeding, rather than quantify transients themselves. Recent advances in multistate, open robust design models are promising in their ability to estimate the occurrence of transients in winter populations

from CMR data (Ruiz-Gutierrez et al. in review), but even these are limited in their ability to distinguish transients from territorial individuals accurately.

In this study, we combined territory-mapping and unmarked survey methods to estimate population abundance, to identify territorial and transient individuals, and to compare the demographic structure of wintering American redstarts. We conducted repeated surveys in Jamaica, where individuals occur at varying densities and across diverse habitats (Sliwa and Sherry 1992, Sherry and Holmes 1996, Johnson and Sherry 2001). Both marked and unmarked methods quantify differences in abundance among habitats. Use of these two survey methods allowed us to test for demographic differences between territorial and transient population components potentially caused by behavioral dominance mechanisms. We tested three predictions about the unmarked method (distance sampling with repeat-counts) compared to territory mapping: It (1) quantifies total abundance of a migratory species efficiently among multiple non-breeding habitats, (2) identifies more individuals by also detecting mobile individuals (transients), and (3) potentially detects individuals of different age and sex structure.

METHODS

Focal species—The American Redstart (*Setophaga ruticilla*) is a widespread, long-distance Nearctic-Neotropical migrant passerine. Its winter range extends from southern Florida through the Caribbean Islands and northern South America, but highest abundances occur in the Greater Antilles (Arendt 1992, Sherry and Holmes 1997). Density, overwinter body condition, and annual survival of redstarts vary among their diverse wintering habitats (Sherry and Holmes 1996, Marra and Holmes 2001, Johnson et

al. 2006). Although they do not commonly sing in winter, redstarts are conspicuous in most habitats due to fly-catching and active gleaning on most substrates, from the ground and foliage to tree trunks and branches (Sherry and Holmes 1997), and agonistic behaviors. Redstarts are often territorial in winter and segregated by sex among habitats (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000). The intraspecific aggression contributing to habitat-use patterns is associated with frequent vocalizations of distinctive (species-specific) “chip” or call notes, allowing reliable recognition by trained observers. Additionally, redstarts use variable social strategies in winter, from strongly site-faithful and territorial to transient (Lefebvre et al. 1992, 1994, Toms 2011, 2013).

Study sites—We chose three habitats in two regions of southwestern Jamaica to compare marked and unmarked methods: mangrove swamp, xeric scrub, and montane wet limestone forest. The mangrove and scrub sites are located in close proximity within the Font Hill Nature Preserve in Westmoreland Parish (UTM 18Q 189082 1997416; 0-1m elevation) and are within 2km of the coastline (Figure 2.1). Hurricanes, woodcutting and cattle grazing periodically disturb these coastal habitats. Mangrove habitats are dominated by black mangrove (*Avicennia germinans*) interspersed with red (*Rhizophora mangle*) and white (*Laguncularia racemosa*) mangrove. Dry logwood (*Haematoxylum campechianum*) scrub sites lie adjacent to, and generally inland from the mangrove forests. This scrub vegetation grows more densely than mangroves, and experiences greater leaf abscission in the dry season resulting in reduced canopy cover (Wilson et al. 2013). Our third research site, in the mountains of northernmost Westmoreland Parish (UTM 18Q 188786 202045; 500m elevation), is one of the few old-growth wet limestone

forest fragments in the region (Figure 2.1). Disturbances here are limited to hurricanes, occasional cattle grazing, and selective logging. The tree community is diverse, including several palm species, Blue Mahoe (*Talipariti elatum*), Kapok (*Ceiba* sp.), African Tulip (*Spathodea campanulata*), and Mahogany (*Swietenia mahagoni*) with a mean canopy height of 20-25m. Dense vine tangles resulting from hurricane damage and treefalls result in a complex, vertically stratified habitat. Over the last four years, this montane region received more than twice the monthly mean precipitation, 220 mm, compared to our coastal sites (91 mm; Jamaican Meteorological Service). All study plots were delimited into 50x50m grids with flagging tape to facilitate mapping individual birds.

Survey methods

Territory-mapping methods— From 2009-2012, we conducted mist-netting, color banding, resighting of banded individuals, and territory mapping of all individuals in the same habitats, research sites and years (see Marra et al. 1993, Parrish and Sherry 1994, Sherry and Holmes 1996, Marra and Holmes 2001, and Studds and Marra 2005 for more details). Daily passive mist netting took place from sunrise to ~1300 hrs in mid January-mid February and again in mid March-early April in long-term net lanes, distributed throughout research plots in mangrove, logwood, and wet limestone forest. We used target netting (intensive mist-netting and call broadcast within a specific territory) to capture individuals observed during mapping or missed during passive netting. Each season, we captured and banded ~70% of the territorial birds present on each site. Captured birds were aged, sexed, and banded with a unique combination of one aluminum and two colored leg bands. Territory mapping (see below) took place from

mid Jan through early April. In wet limestone forest habitat we followed a similar banding schedule in January and February, and conducted periodic target netting from mid-February through early April, between unmarked survey intervals.

While mapping observations from early January to late March (ending more than a month prior to departure and migration), we recorded locations and movements of both banded and unbanded birds on gridded sites (at 50m intervals). Once located, a bird was followed from a distance (so as not to influence its behavior) and its movements recorded. For all birds, we noted age, sex, color bands (if applicable), and distinguishing plumage characteristics, if unbanded. All movements were mapped onto a study plot grid, along with any aggressive interactions with other birds. Observers followed an individual bird for up to 30 min or until lost, mapping as much area used as possible. We attempted to acquire at least 10 separate observations/territorial bird on different days between January and April. Once we accumulated repeated observations of individual birds, we generated a two-dimensional map for each habitat, from which the number of territorial birds/ha was estimated. Transient individuals were not included on these maps. We incorporated individuals whose territories were estimated to overlap at least 25% with the edge of study plots in these calculations, because these edge birds were detectable by point-count surveys. Observers typically identified and mapped the remaining unbanded territorial individuals on a given site (10-30%) using diagnostic plumage markers (black patches, brightness of orange pigment; Sherry and Holmes 1992, Lemon et al. 1992, Reudink et al. 2009b) and territorial behaviors (calling within consistent area). This allowed us to include these birds in territorial density estimates. However, 10-30% is a best estimate, because we are unable to distinguish all unbanded

territorial individuals from transients. This uncertainty highlights the importance of the present study, namely to gain a more accurate estimate of how many unbanded individuals documented on territory maps are un-captured residents versus transients.

Unmarked survey methods—We distributed 20 point-count locations in mangrove and wet limestone sites, and 15 in logwood scrub, choosing locations that allowed 100m between each survey point and at least 50m from a habitat edge. We repeated distance-sampling surveys (Buckland et al. 2001) at every point-count location, giving two periods per point in mid- to late winter (early-mid February and late March-early April) (Kéry et al. 2005, Lyons et al. 2012). By January, territorial individuals have established territories and typically persist at these locations up to the time of northward migration (Marra and Holberton 1998, Marra 2000). One experienced observer (AMP) carried out these surveys in all years, along with one new observer each year trained by AMP to recognize species-specific winter vocalizations. Approximately 60% of detections were vocal, rather than visual.

We adapted distance-sampling survey protocols from Buckland et al. (2001) by using a single observer per sample point to record all redstarts detected, age and sex if possible, type of detection (seen/heard), and estimated distance (m) from observer for each individual bird within a ten-minute survey period. We classified birds detected at >50m as outside the survey boundaries, due to difficulty of redstart chip note identification beyond this range (AMP pers. obs.).

Quantifying transient individuals via territory-mapping methods

We expanded on the methods of Latta and Faaborg (2001) to quantify the occurrence of transient birds. We crosschecked banded individuals with seasonal territory maps to determine if the individual was recorded occupying a territory within the same or a neighboring study site. Individuals inhabiting no territory were classified as transient, i.e. non-territorial *within that site*, and assumed to have no territory or possibly one outside that site. These banding records also allowed us to compare the age and sex distributions of territorial vs. transient individuals.

In 2010, we had a larger field crew and mapped the locations of more birds on our plot grids. This allowed us to detect most of the transient birds present on the plots. We classified an individual as a banded transient if it was resighted at least once, but did not hold a territory. While we are not certain that these individuals did not hold territories off our study plots, they could be classified as ‘wanderers’ or transient on our plots. The intensive mapping effort in 2010 allowed us to estimate numbers of these individuals directly, which we tallied for a given site from Jan-Mar and added to estimates of territorial birds (described above). This combined estimate accounted for *all* banded individuals present on our plots, thereby generating a best estimate of **total** redstart density to compare with the 2010 distance-sampling (unmarked) survey estimates.

Statistical methods

Distance-sampling data analyses—To estimate densities via the unmarked method we used package *unmarked* in program R (R Core team. 2013), which incorporates the multinomial-Poisson mixture model of Royle et al. (2004) and allows modeling of density and detection probabilities (Chandler 2011).

We treated spatial variation in redstart number at each point count (N_i) as a Poisson random variable (λ_i) for the abundance distribution. We modeled the detection process using traditional distance-sampling likelihoods for point count data (Buckland et al. 2001). We tested the fit of both half-normal and hazard-rate detection functions, using model-selection methods to choose the hazard-rate function (Table 1). This function assumes that detectability declines less precipitously initially than half-normal functions, allowing for similar detection likelihoods in the closest (0m, 12.5m) detection distance intervals. We estimated distance as a continuous variable in the field, but considering that most observations were based on auditory detections, we used larger distance intervals of roughly $\frac{1}{4}$ the maximum detection distance, or 12.5 m, in the models. Our distance-sampling model integrated the hazard-rate detection function (σ) over each of these distance intervals to derive detection probabilities. The model used log-link functions to incorporate environmental covariates for abundance (λ_i) and detection (σ_i) (See Royle et al. 2004, Sillett et al. 2012 for further details of models; Sample R code is provided in the Appendix). Habitat and year were considered covariates for abundance, and habitat was used as a covariate of detection.

We used AIC model selection to evaluate candidate models of redstart density. After identifying the top model, we used parametric bootstrapping and ran 150 simulations, using a chi-squared test to assess the goodness of fit (Chandler 2011). For this analysis, a p-value of 0.5 represents a perfect model fit indicating bootstrap estimates were neither too high nor low. We compared predicted abundance for each habitat and year from the top model to density estimates from territory mapping.

Age and sex analyses- To compare age and sex distributions between territorial and transient individuals, we used chi-squared tests of the frequencies of males (M) and females (F), and separately of second year (SY) and after-second year (ASY) individuals. These frequencies were calculated from capture and territory mapping datasets.

RESULTS

Abundance estimation via unmarked and territory-mapping methods

The best unmarked (distance-sampling = D-S) model included both habitat and year effects on both density and the detection process (Table 2.1). Parametric bootstrapping simulations and a chi-squared goodness-of-fit test indicate that our top model provided sufficient fit to the dataset ($P = 0.76$). Model outcomes indicate that local population density of redstarts varied both by habitat and year. Mangrove habitat had the highest densities and greatest annual fluctuations, wet limestone the lowest density, and both wet limestone and logwood the smallest annual changes (Figure 2.2, D-S estimates).

Estimated redstart densities from the best-fit unmarked model were greater than density from mapping marked territorial redstarts across all habitats and years except for mangrove in 2011 (up to 40% difference in estimates; Figure 2.2), indicating that point counts either overestimated redstart density or detected individuals that territorial estimates missed. Differences between point count and mapping estimates were significant all three years in dry scrub habitat, two of three years in mangrove, and one year in wet limestone. In 2011, the year with the highest overall redstart abundance, territorial densities increased in this year and overlapped with distance-sampling estimates.

Evidence for the detection of transient individuals

Habitats in which point count densities differed most from those based on territory mapping of banded redstarts (dry scrub and mangrove; Figure 2.2) also had the highest occurrences of transient individuals (Figure 2.3). In the wet limestone habitat, where transient individuals were rare (8 individuals in three years), unmarked and territory mapping methods produced similar abundances. We identified 53 marked transient individuals in 2010 (26 in logwood, 27 in mangrove), calculated using banding and daily territory mapping data. Adding these individuals to the marked abundance estimates for a given habitat resulted in densities that no longer differed significantly between the two methods (Fig. 2.4). These results imply that unmarked methods detected transient birds in these habitats rather than double-counting territorial individuals.

Demographic structure of territorial vs. transient individuals

Based on data from marked individuals, age and sex composition of redstarts differed between territorial and transient individuals for all three habitats in some years. Transient populations tended to be composed of more females in both dry scrub and mangrove habitats (Table 2.2, Figures 2.5A, C). Proportionately more SY males were transient in mangrove habitats in 2010 and 2012 (Figures 2.5A, C). Territorial populations in mangrove were male-dominated, typically with a greater proportion of ASY individuals. In 2011, a large influx of young males caused a shift in age-sex ratios, resulting in more SY males than females in both transient and territorial populations of dry scrub and mangrove habitats (Figure 2.5B). Transient individuals, primarily females, were only present in the wet limestone habitat in 2012, and totaled no more than 7

individuals. Territorial males (ASY and some SY) dominated this habitat largely to the exclusion of females (Figure 2.5C, Table 2.2).

TABLES

Table 2.1 Basic distance model results for combined sample data collected in 2010-2012. Environmental covariates indicated by λ for abundance and σ for detection process.

Model	# Parameters	AIC _c	Δ_i	w_i
$\lambda(\text{Habitat}+\text{Year}) \sigma(\text{Habitat}+\text{Year})^b$	11	2193	0	0.99
$\lambda(1) \sigma(\text{Year} + \text{Habitat})$	7	2202	9.11	<0.01
$\lambda(\text{Habitat}+\text{Year}) \sigma(\text{Habitat})$	9	2212	19.1	<0.01
$\lambda(\text{Habitat}+\text{Year}) \sigma(.)$	7	2217	24.2	<0.01
$\lambda(\text{Sample}+\text{Habitat}) \sigma(.)$	10	2220	26.8	<0.01
$\lambda(\text{Sample}+\text{Habitat}+\text{Year}) \sigma(.)$	12	2224	30.9	<0.01
$\lambda(\text{Habitat}) \sigma(\text{Habitat})$	7	2234	41	<0.01
$\lambda(1) \sigma(\text{Year})$	5	2236	42.9	<0.01
$\lambda(\text{Habitat}) \sigma(.)$	5	2239	46.1	<0.01
$\lambda(.) \sigma(\text{Habitat})$	5	2247	54	<0.01
$\lambda(\text{Year}) \sigma(.)$	5	2258	65.2	<0.01
$\lambda(\text{Sample}) \sigma(.)$	8	2260	67.8	<0.01
$\lambda(\text{Sample}+\text{Year}) \sigma(.)$	10	2264	71.8	<0.01
Hazard-rate: $\lambda(.) \sigma(.)$	3	2280	87.5	<0.01
Half-normal: $\lambda(.) \sigma(.)$	2	2289	96.3	<0.01

^a Δ_i =change in AIC_c values; w_i indicates model weight.

^b Chi-squared GOF, p-value= 0.86.

Table 2.2 Territorial vs. non-territorial age and sex distributions of redstarts within a given year and habitat. Chi-squared tests were used to compare frequencies of age and sex classes (adults and second-years, males and females) within a habitat type and year.

Note: Transients only present for comparison in wet limestone in 2012.

Year	Habitat	χ^2 value	D.F.	P-value
a. Age				
2010	Logwood	1.21	1	0.27
	Mangrove	0.18	1	0.67
2011	Logwood	1.4	1	0.24
	Mangrove	0.99	1	0.32
2012	Logwood	1.14	1	0.29
	Mangrove	0.2	1	0.65
	Wet Limestone	0.33	1	0.93
b. Sex				
2010	Logwood	5.56	1	0.02*
	Mangrove	2.511	1	0.11
2011	Logwood	1.22	1	0.27
	Mangrove	5.32	1	0.02*
2012	Logwood	2.2	1	0.14
	Mangrove	0	1	0.98
	Wet Limestone	3.11	1	0.08

*P<0.05

FIGURES



Figure 2.1 Map of field site locations in Jamaica. (Circle-star) indicates location of coastal field sites (mangrove and dry scrub), (Star) indicates location of wet limestone forest site in montane interior.

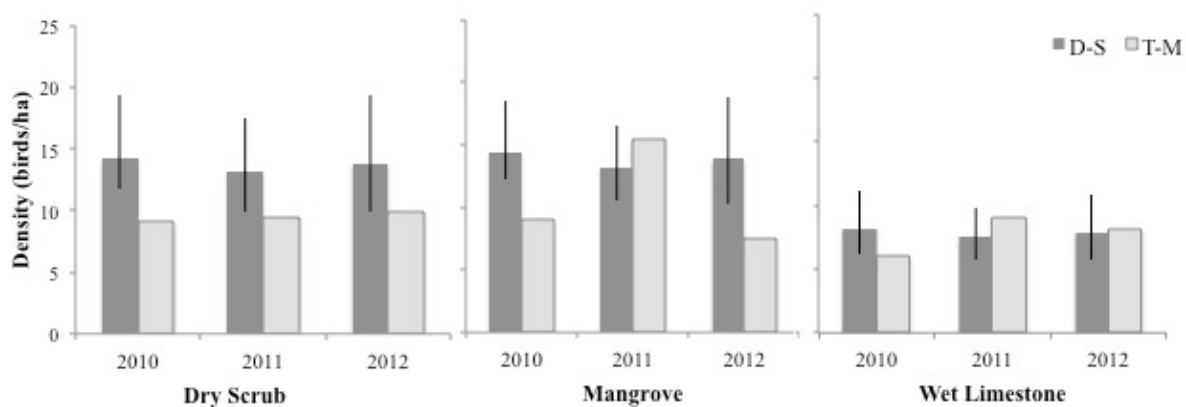


Figure 2.2 Comparison of predicted densities calculated via distance-sampling (D-S) and territory mapping (T-M); the latter do not include transient individuals. Distance sampling densities derived from best model of candidate set (Table 1). Error bars indicate 95% confidence intervals.

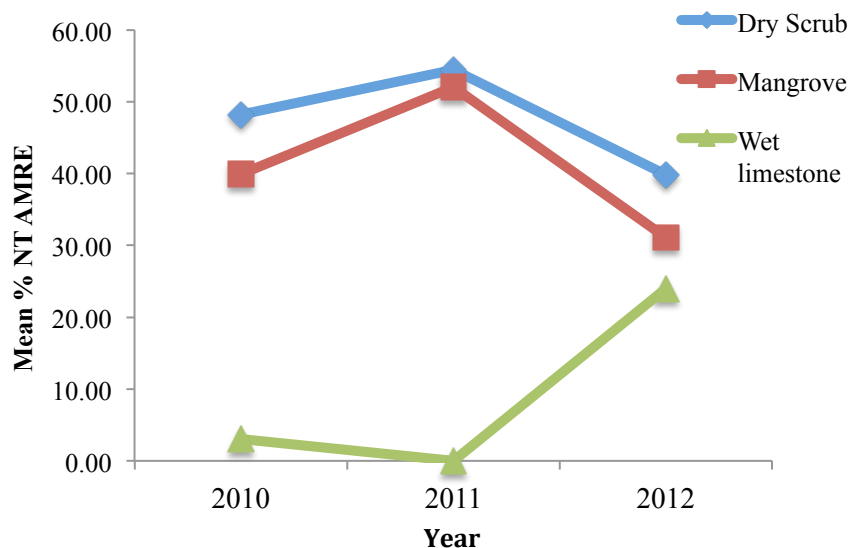


Figure 2.3 Percentages of captured redstarts that were non-territorial transients (NT), i.e., captured within a habitat and not subsequently observed to hold a territory in that location from 2010-2012.

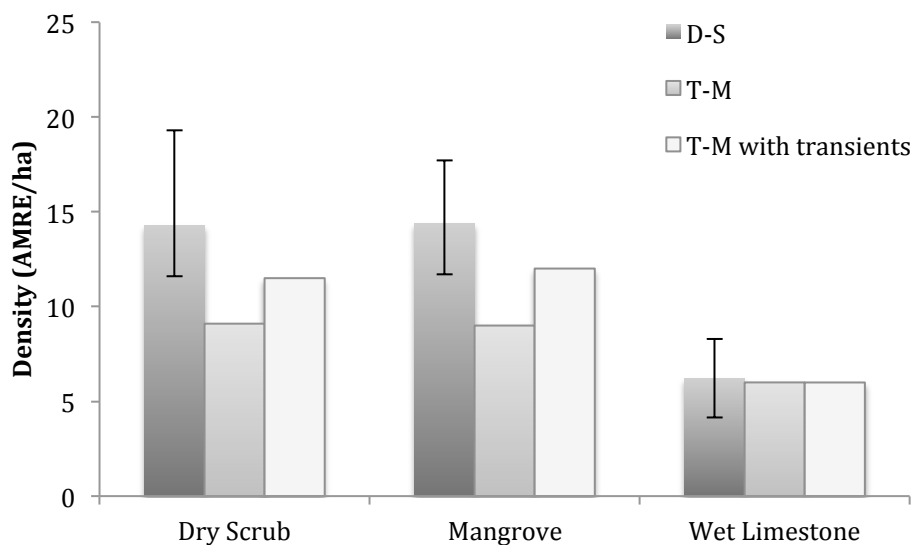


Figure 2.4 Comparison of 2010 density estimates from distance-sampling (D-S), territory mapping (T-M) and a third method that produces a *total* density estimate that includes non-territorial birds detected during daily site mapping throughout the winter season.

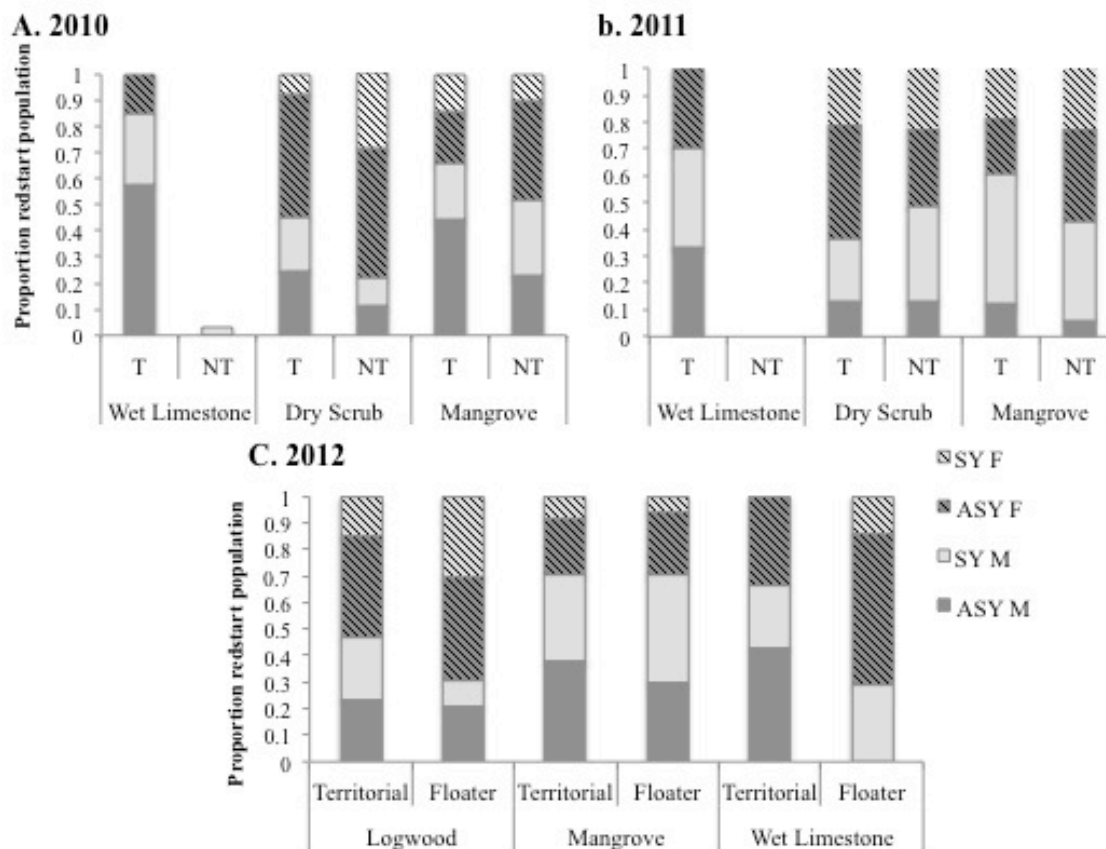


Figure 2.5 (A-C) Comparison of age and sex of captured *territorial* and *non-territorial* redstarts in 2010 (A), 2011 (B), and 2012 (C). Species age codes: SY, second year bird; ASY, after second year. Sex codes: F, Female; M, Male.

DISCUSSION

Both unmarked and territory-mapping methods can estimate abundance or density, if the portion of the population being measured is clearly defined. The unmarked method generated estimates of total population density and abundance that included transients and individuals with multiple behavioral strategies. Territory mapping methods distinguished between transient and territorial individuals and provided demographic data showing that proportionally more subordinate (females and young, depending on habitat and year) and transient individuals were likely detected by unmarked methods. Unmarked survey methods thus generated an estimate of total population size, independent of space-use strategy. Intensive banding and mapping methods provided an estimate of the density of territorial individuals, as well as demographic information for all birds, transient and territorial alike. Each of these methods has limitations, but combining them provides better resolution of transient distribution, abundance, and demography among diverse habitat types.

Unmarked methods do not provide demographic information or means of distinguishing between territorial and transient individuals. These methods also rely heavily on detecting birds via their vocalizations, and have rarely been used to survey bird populations outside the breeding season. Application of unmarked survey methods to breeding passerines have attributed differences between point-count and territorial density estimates to the use of longer survey durations or smaller observation radii (Cimprich 2009, Reidy et al. 2011). These can potentially increase the number of individuals observed, due to high song rates and greater detectability close to the observer (e.g., Staicer et al. 2006). The first concern, double counting individuals due to transient

movement between point-count locations, is possible, but we detected no major shifts in the numbers of transients throughout the season (sample timing was not a significant covariate), suggesting that transients likely have a limited home range and remain in the same region throughout the winter. Transients were abundant throughout scrub and mangrove habitats, thus occasional double-counting is unlikely to produce a marked bias in abundance estimates, as would be the case if transients were few and patchily distributed. Additionally, winter vocalizations are limited to “chip” call notes, and a high percentage of our observations came during the last half of the ten-minute survey period (AMP, unpubl. data). Therefore, a shorter survey interval would likely lead to underestimates of redstart density in Jamaican habitats.

Marked methods are precise and detailed in terms of territorial density and individual identity (e.g., age, sex), but are time- and resource-intensive. Marked methods in our study system required 1000+ person-hours per season to generate the territory maps necessary for accurately estimating density and abundance in two habitats (~35 ha in total), whereas point counts only required ~150 person-hours per season. Additionally, identifying and counting transient individuals with these methods is possible for marked individuals, but even more difficult and time-intensive, and thus rarely done. Accurate estimation of the abundance of unmarked individuals during territory mapping operations is unreliable at best. This highlights the importance of carefully considering the type of data needed, especially with regard to identifying territorial versus transient individuals, or both.

Although we operationally distinguished territorial and transient individuals in all our habitats, additional social strategies, from regular local movements (Smith et al.

2011) to complete transience (Wunderle et al. 1999, Toms 2011, 2013), blur the line between these groups, suggesting more of a continuum of wintering space- and resource-use strategies. A small number of redstarts (< 5%) were annually documented occupying multiple, spatially separated territories on our mangrove and scrub research plots, while other individuals vanished mid-season and returned in subsequent years (<5%). Redstarts elsewhere than Jamaica, and other migratory passerine species indicate a similar range of space-use patterns during the non-breeding season (Lefebvre et al. 1994, Lefebvre and Poulin 1996, Brown and Sherry 2008, Smith et al. 2011, Lenda et al. 2012). Methods are needed that can efficiently estimate density and abundance of all individuals across diverse habitats. The agreement between our methods, once transients were added to marked individuals (Fig. 3), suggests that unmarked methods are a more efficient and potentially less-biased method for estimating the total numbers of redstarts. Point counts apparently missed few of the birds present, regardless of their overwinter space-use strategy. However, population studies often require more detailed information on individual birds' status, and we argue that point count and territory mapping approaches are complementary. Unmarked methods can be applied across a large spatial area and multiple habitats, while marked methods can sample detailed demographic data from a few key sites that can help partition individuals into territorial versus transient.

Our study also revealed unexpected differences in population density and demography among habitats. The results supported our expectation that most transient individuals would be young males and socially subordinate females (Marra 2000). Mangrove and scrub plots had similarly high occurrences of transient individuals and high densities of redstarts generally, but varied in their age-sex ratios. Wet limestone, by

contrast, had few transient individuals in most years ($< 5\%$) and the lowest densities of redstarts overall, but also the greatest proportion of socially dominant (ASY male) individuals. This is consistent with previous findings (Johnson et al. 2006) that habitats differ qualitatively, in terms of the size and social structure of the redstart populations they support, and that these characteristics may be linked to behavioral mechanisms, as well as environmental factors that fluctuate annually. However, these results were also surprising, because differences in numbers of transients correspond most closely with variation in rainfall among inland (wet limestone forest) and coastal (mangrove and scrub) regions. While we know that sexual habitat segregation plays a role in the demographic distribution (Marra 2000, Townsend et al. 2012) and abundance of migratory passerines across non-breeding habitats (Wunderle 1995, Johnson et al. 2006), our data suggest that rainfall patterns may also contribute to alternative behavioral mechanisms, such as transience or multi-territoriality among habitats (Brown and Long 2007).

For our study, we defined ‘transients’ and ‘non-territorial’ birds as individuals that were observed and documented on our research sites, but held no territory therein. This does not preclude the possibility of these individuals maintaining territories elsewhere, although the different age- and sex-composition suggests possibly different wintering strategies. An important next step will be to track these individuals across multiple non-breeding habitats, while monitoring extrinsic environmental changes, e.g. rainfall and food availability. Such tracking will provide clearer estimates of the specific over-wintering strategies used by these ‘transient’ individuals, and improve abundance estimates. Another need is to estimate survival of transient versus territorial individuals.

Such information may help explain variation in redstart habitat use and population limitation in non-breeding landscapes.

Our understanding of wintering migrant populations and social systems will benefit from future analytical methods that combine information from disparate sources, such as distance sampling of unmarked populations and intensive territory mapping. For example, we could not provide variance estimates for the proportions of transients within a plot and year. Integrating marked individuals into estimates of abundance will involve tradeoffs of effort. For example, Ruiz-Gutierrez et al. (in review) used CMR data to estimate movement and transience of multiple passerine species in winter. These methods estimate when and for how long a transient remains in a population. Currently, the approach we used only provides a seasonal estimate of the number of transients in a given site. However, open population models based solely on CMR classify individuals as transient based on capture histories, rather than on behavioral data. Recapture probabilities of transients are often low so that relying exclusively on these histories could result in misclassifying individuals as transients that are actually territorial but not detected after first capture, e.g., because of holding a territory at the margin of a study area. While more time and resource-intensive, the combination of unmarked and territory-mapping methods holds promise for increasing our knowledge of transient demography, distribution, and role in population dynamics.

Chapter 3

Habitat suitability determines non-breeding season distribution and demography of a migratory songbird at multiple spatial scales

ABSTRACT

Global declines of migratory birds have focused conservation efforts on habitat loss and degradation – both on breeding and non-breeding areas. However, our understanding of how demography varies among tropical habitats is poorly known for most avian species. Such knowledge is critical for furthering our understanding of population dynamics in habitat generalist species and making informed land management decisions. We assessed the suitability of six distinctive habitats, within 2 regions, three within the coastal region (mangrove, dry scrub, dry limestone) and three within the inland region at higher elevation (wet limestone forest, coffee, and citrus), for migratory American redstarts (*Setophaga ruticilla*) overwintering in Jamaica using a series of intrinsic indicators (transience, survival, spring departure date, transience, age, and sex) and extrinsic, or environmental conditions (rainfall and food availability). Our results indicate that habitat quality gradients occur at multiple spatial scales, based on intrinsic indicators of habitat suitability for redstarts. Regionally, redstarts occupying inland habitats experienced significantly higher survival and lower proportions of transients suggested higher suitability than the coastal region. This corresponded with higher winter rainfall in the inland habitats. Within regions (locally), wet limestone (inland) and mangrove (coastal)

seemed to be the highest suitability habitat as evidenced by higher food availability, a higher proportion of males, and earlier spring departure dates. Densities of redstarts corresponded with rainfall and were significantly higher in the low suitability coastal region. However, density did not correspond to local (within region) variation in habitat quality, suggesting that it is not a reliable indicator of suitability at this scale. Given the importance of moisture as an underlying driver of habitat suitability, redstart populations are likely vulnerable to current and projected declines in rainfall. Conservation efforts should consider targeting the preservation of tall wet forests, which simultaneously preserve both migratory and resident species.

INTRODUCTION

Globally, migratory bird populations are declining (Newton 2004) and habitat loss, combined with climate changes throughout the annual cycle, are predicted to exacerbate this trend (Calvert et al. 2009, Newbold et al. 2014, State of the Birds 2014). Habitat loss and conversion constrains organisms to increasingly limited areas. Over two-thirds of the 14 major terrestrial biomes on Earth were degraded by 2000, primarily from agricultural cultivation (MEA 2005). In the face of such rapid change, we still have a limited understanding of the importance of many disappearing habitats for maintaining species (Hoffman et al. 2010, Latta 2012, Caplins et al. 2014).

How population dynamics are influenced by habitat suitability, particularly for migratory species throughout their annual cycle, is poorly understood. Suitability can

affect the fitness of organisms through variation in extrinsic (environmental) conditions such as resources, predation pressures, and climate (Pulliam et al. 1992, Johnson 2007). For example, food resource availability in tropical winter habitats can influence intrinsic indicators of population performance like over-winter body condition, subsequent breeding season events, and annual survival of migratory bird species (Marra 1998, Norris et al. 2004, Gunnarsson et al. 2005, Gordo et al. 2007, Reudink et al. 2009a, Thaxter et al. 2010). However, migratory species often occupy a wide array of habitats and studies of winter ecology typically focus on too few habits, limiting our understanding how tropical habitats can vary.

Habitat use can be constrained by preemptive settlement and intraspecific competition in species with despotic distributions (Fretwell and Lucas 1970, Rosenzweig 1991). Such mechanisms lead to regulation of population growth and abundance according to the extent of suitable habitats (Gill et al. 2001, Rodenhouse et al. 2003, Kokko et al. 2004). Despite the emerging evidence of the importance of habitat suitability during the non-breeding season for individual performance and population dynamics, our knowledge of which habitats are most suitable for migratory birds during the non-breeding season remains poorly known for most species.

Understanding habitat suitability is handicapped by the difficulty of identifying and measuring environmental conditions (e.g., food availability, predation). Food availability is often difficult to measure, given insufficient knowledge of dietary preferences for many migratory species (Poulin and Lefebvre 1996). For generalist insectivorous species, sampling arthropods among structurally and floristically diverse habitats is challenging, particularly given that abundances can vary at small spatial scales

(Smith and Rotenberry 1990, Cooper et al. 2012). However, rainfall and moisture levels correlate with differences in food variability among habitats and climate affects are another means of assessing habitat suitability (Smith et al. 2010, Wilson et al. 2013, Ockendon et al. 2014). Predation also affects suitability, primarily by limiting nesting success of migratory species (Chalfoun et al. 2002, Holmes 2007).

Assessing relative suitability of different habitats is also complicated by behavioral characteristics of the birds themselves. For example, territoriality and behavioral dominance help structure patterns of habitat occupancy for many species of migratory passerines, and can limit access to more suitable habitat for subordinate individuals (Newton 1998, Price and Gross 2005). Dominance behavior relegates subordinates, typically females and younger individuals, to territories in low quality sites or to a non-territorial strategy (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000). As a result, site-persistence declines and transience increases in these subordinate classes and/or birds inhabiting low quality sites (e.g., Brown and Long 2007, Brown et al. 2008, Kresnik and Stutchbury 2014). A comprehensive assessment of habitat suitability for a migratory passerine must account for the consequences of territorial behaviors, as well as environmental conditions, on intrinsic indicators of population performance. Such factors contribute to both the size and persistence of populations (Newton 1998, 2004, Johnson 2007), and have been used in a variety of ways by past researchers to help identify the most suitable habitats.

Transient or non-territorial individuals can provide valuable information about habitat quality, although this has been examined infrequently; for example they are not mentioned in Johnson's (2007) review. Transient individuals can indicate higher or

lower habitat quality, depending on a species' behavioral space-use mechanisms (e.g., Lefebvre et al. 1994, Penteriani et al. 2005, Brown and Long 2007, Lenda et al. 2012). For despotic species, greater abundances of transients should occur in habitats of lower relative suitability (Wunderle 1995, Latta and Faaborg 2001, Smith et al. 2011). While transience has been documented frequently in migratory species during the winter season, few studies have compared distributions or abundances of transient individuals with other intrinsic indicators of habitat suitability (Lefebvre and Poulin 1994, Latta and Faaborg 2001, Brown and Long 2007, Brown and Sherry 2008).

Demographic variables such as age and sex ratio can indicate habitat quality. High ratios of males usually indicate high quality habitat for species with sexual habitat segregation (Marra et al. 1993, Marra 2000, Latta and Faaborg 2002). However, females do not always exhibit poorer condition from occupying different habitats than males. In some cases, females survive equally well, despite inhabiting seemingly low quality sites (Wunderle 1995, Catry et al. 2004), although this could be a year effect related to varying rainfall conditions. Age ratios can also indicate habitat suitability, with older, more dominant individuals occupying higher quality habitats (Marra 2000, Latta and Faaborg 2002), but this also varies considerably by species. Given these inconsistencies, age and sex ratio measures also warrant comparison to more direct measures of individual condition in interpreting habitat quality.

Additionally, individual condition at the end of the non-breeding period influences when migratory birds can depart (Marra et al. 1998, Studds and Marra 2007, Cooper et al. 2015) and subsequently arrive (Gordo et al. 2005) on their long-distance migration from Neotropical winter habitats for breeding grounds. Early arrival time on

breeding grounds increases reproductive success (Reudink et al. 2009b, Finch et al. 2014) through access to better breeding territories, earlier egg-laying dates, and greater reproductive success for both males and females. This indicates how winter conditions can carry over to affect not only individual condition but also fecundity in the breeding season. Understanding spring departure timing in relation to other intrinsic indicators of winter condition has consequences for the entire annual cycle.

Annual apparent survival is a critical and relatively direct indicator of habitat suitability (Johnson et al. 2006, Grande et al. 2009, Cresswell 2014), though difficult in practice to estimate accurately. It provides strong evidence of individuals overall performance (Duriez et al. 2012, Lopez-Lopez et al. 2014), and is particularly compelling when used in conjunction with other intrinsic measures of suitability (Sherry and Holmes 1996, Johnson 2007).

Finally, abundance and density were some of the first criteria used to assess habitat suitability in birds (Kluyver and Tinbergen 1953, Glas 1960). Ideal free distributions among habitats predicted a positive relationship between abundance in different habitats and suitability (Fretwell and Lucas 1970, Sherry and Holmes 1996, Sutherland 1998). Yet many migratory species are territorial in winter, which results in despotic distributions (Fretwell and Lucas 1970, Rosenzweig 1992, Sherry and Holmes 1996, Sutherland 1998). For such populations, habitat suitability is negatively related to density, because intraspecific competition for space and resources excludes individuals from better habitats and thus limits density. However, other evidence suggests density is often decoupled from habitat suitability and individual condition in migratory passerines (Marra and Holmes 2001, Pidgeon et al. 2006, Chalfoun and Martin 2007, Johnson et al.

2011). Because of this, it is critical to compare density with other intrinsic redstart indicators and environmental conditions to understand whether it is an accurate reflection of habitat suitability (Johnson 2007).

Here we compared a series of intrinsic indicator variables with environmental conditions in six tropical winter habitats, which are located within two different regions (inland and coastal). We focused on a migratory bird species, the American redstart (*Setophaga ruticilla*), which is territorial and exhibits despotic habitat occupancy. First, we quantified environmental conditions (rainfall and food availability) among habitats and tested the hypothesis that these corresponded to variation in proportions of transients, age and sex ratios, spring departure dates, and survival, both within and between regions. Second, we tested the hypothesis that redstart density is inversely related to habitat suitability and thus corresponds with other intrinsic indicators of habitat suitability.

METHODS

Study species – We studied the American Redstart, a Neotropical-Nearctic migratory passerine that winters primarily in the Caribbean, Central America and the northern sections of S. America (Arendt 1992, Sherry and Holmes 1997). Redstarts are a good species for investigating habitat suitability because they use diverse habitats, e.g., wintering in virtually every habitat available in Jamaica (Sliwa and Sherry 1992). Additionally, behavioral mechanisms influencing winter habitat distributions of redstarts are well studied, particularly in coastal habitats (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000), guiding inferences about relationships between demography and

habitat suitability. Redstarts are mobile, aerial insectivores, feeding almost exclusively on arthropods (Sherry and Holmes 1997).

Habitats – Our study sites were widely distributed in southwestern Jamaica.

Environmental data came from six different habitats, four native (wet and dry limestone forests, mangrove, and dry scrub) and two agricultural (coffee and citrus). Three are located in the central montane interior region (wet limestone forest, citrus, coffee) and the remaining three in the coastal region (Figure 1). We collected environmental and density data, including rainfall, food availability, and vegetation characteristics, from all six habitats, and more intensive data on fitness consequences of habitat occupancy from four: wet limestone, mangrove, dry scrub, and citrus.

Field methods

Field work extended from early January through early May, when spring departure was completed. We collected data on all demographic variables from 2009-2012 and for survival and rainfall data, 2009-2013. Arthropod and vegetation data came from 2010-2012.

Intrinsic population indicators

Bird density and transients – We used a combination of mark-recapture-resight and territory mapping methods to estimate density of territorial individuals in our four intensive habitats – citrus, wet limestone forest, mangrove, and scrub (see Marra et al. 1993, Sherry and Holmes 1996, Studds and Marra 2005 for details). We used passive and target-netting methods annually to capture and band as many territorial birds as possible, from mid-January to late March. We used unique combinations of one aluminum and

two color bands to distinguish individuals once released. We resighted and mapped territories from mid-January to early April, and generated summary maps for estimating territorial density per habitat.

However, we also quantified density among all six habitats independently using point-count survey methods. We used distance sampling (Buckland et al. 2001) and repeat-count protocols (Kery et al. 2005). Twice annually, in mid-winter (Feb) and early spring (late March-early April), we re-surveyed twenty points in each habitat with the exception of scrub (15 counts). We used these point-count data to estimate total density, i.e. territorial and non-territorial (henceforth transient) individuals. Compared with territorial estimates from mapping methods, these gave an estimate of number of transient (= non-territorial) individuals (Peele et al. in review). We also verified the presence of these transient individuals using capture records and territory maps for 2009-2012.

Demographic and population variables –Mark-recapture-resight and territory mapping methods also allowed us to estimate demographic rates, including age and sex ratio and spring departure schedule, as well as annual apparent survival. Age and sex determinations are based on Pyle (1997) and Marra et al. (1993). We used summary maps to monitor departure timing of territorial individuals from April 15 to 2nd week of May. We visited each individual's territory daily in three-day rounds in mangrove and scrub sites. Due to time constraints, we only visited citrus territories every other day, but feel this did not bias results given the relative ease of detection and identification of banded individuals in this habitat. Time spent searching a territory-increased daily until day three, when we played a short 60 sec burst of conspecific call and song. If we did not observe a bird after two of these 3-day sessions, it was classified as departed as of the

beginning of the second missed time period. We calculated the proportion of the population departed from each habitat by May 6th for subsequent comparison among habitats and years. Finally, we used the capture-mark-recapture data to estimate apparent annual survival from 2009-2013. We were not able to collect sufficient data on physiological condition for all habitats, but this allowed us to collect our population and environmental data in a greater range of habitats.

Environmental variables – Three environmental variables were quantified that are relevant to an insectivorous bird wintering in the Caribbean: rainfall, arthropod availability, and vegetation volume data, the latter two sampled twice annually in mid-winter (Jan-mid Feb) and early spring (late March-mid April). The Jamaican Meteorological service provided monthly mean rainfall, from weather stations located within 5 km of all field sites.

We collected arthropod samples using a standardized sweep-net protocol (Cooper et al. 2012): 20 sweeps with a 3m pole through accessible foliage. We bagged and froze sweep net samples, then sorted arthropods under a microscope. We identified these to order, quantified abundances, and preserved all in ethyl alcohol vials. After each season we oven-dried and weighed all samples (to 0.0001 g) using standard protocols (Studds and Marra 2005).

Vegetation structure was estimated from foliage height profiles (Wunderle 1999, Suarez-Rubio and Thomlinson 2009) taken at 5 points for each survey location (center and 5m from the center in each cardinal direction). Using a 3m pole marked every half meter, we estimated the presence of foliage for seven height intervals: <0.5, 0.5-1, 1-3, 3-5, 5-10, 10-15, 15-20m. We created an index of vegetation volume for each survey

location based on averaging the number of height intervals with foliage at each of the 5 points.

We sampled vegetation and arthropods at twenty points per habitat (except only 15 in dry scrub), corresponding to bird survey point locations; we then multiplied each arthropod sample by the corresponding mean vegetation index score to correct for differences in vegetation volume both within and among habitats.

Statistical methods

Survival Analysis – Using rMark in program R (R Core Team 2013), we fit our data to Cormack-Jolly-Seber models (Lebreton 1992) to estimate annual apparent survival. We assessed goodness of fit of the global model, finding no evidence of overdispersion in our data. We then used a hierarchical approach, first parameterizing models for detection rate (p) as a function of age, sex, habitat, time, and then used the top model to identify important survival (ϕ) covariates. These variables included age, sex, habitat, mean winter rainfall, conspecific density (bird/ha), and food availability. We ranked models according with second-order Akaike's information criterion (AICc) and associated likelihood with AICc weights (w_i , Burnham and Anderson 2002). Finally, we used model averaging to generate annual apparent survival estimates by region, habitat and year.

GLMMs – We used generalized linear mixed models to assess variance of demographic variables over time and among habitats, as well as to test relationships between several response (age, sex ratio, and departure timing of territorial individuals, proportion of transients) and predictor variables (region, habitat, rainfall, food

availability; also age and sex for the latter two response variables). We used AIC and r^2 values to rank models. We tested the significance of each predictor variable in the top model by iteratively removing it from the full model and comparing the two with an ANOVA test with one degree of freedom. All analyses were done in program R.

Food analyses- to assess variation in environmental conditions among habitats, we estimated the relative heterogeneity of arthropod biomass (g/sample) as the coefficient of variation for each habitat. We used this as a proxy for food predictability. Additionally, we calculated arthropod abundance change from early to late winter. The distribution of these data was extremely non-normal and could not be transformed or corrected to achieve normality, thus we used a non-parametric Kruskal-Wallis test of variance to compare over-winter change in arthropod biomass with time (year), habitat type, and rainfall variables. We used post-hoc Nemenyi tests to identify which habitat pairs were significantly different.

Point-count (Unmarked) Analysis – Using hierarchical distance sampling methods (Royle et al. 2004), we estimated density from point-count survey data (See Chandler 2011, Sillett et al. 2012, and Chapter 2 for further details). Initially, we combined survey data for all habitats and years into one summary dataset, and generated models including several environmental covariates (rainfall and arthropod biomass). Using AIC model-selection, we identified the top model ($\Delta AIC < 2$) and assessed it using a chi-squared goodness of fit (GOF) test. However, given the size and inherent variability of this summary dataset, the GOF score ($p > 0.95$) was too high to generate density estimates from this top model. We then analyzed each habitat individually, which produced acceptable GOF scores for top models in all habitats (Table 2). From these models, we

generated density estimates and used 95% confidence intervals to assess differences among habitats.

RESULTS

Environmental predictors of demographic and distributional variation

Regionally, inland habitats experienced the highest winter rainfall every year from 2009-2012 (Figure 3.2). Wet limestone forest had the highest mean rainfall in winter overall, followed by citrus. Coastal mangrove and scrub habitats experienced an extreme drought each winter. Contrastingly, mean food availability varied significantly among neighboring habitats: citrus - wet limestone: $t\text{-value}=4.81$, $DF=118$, $p\text{-value}<0.001$; mangrove - scrub: $t\text{-value}=3.16$, $DF=103$, $p\text{-value}<0.003$ (Figure 3.3), and typically corresponded with higher proportions of males, earlier spring departures, and fewer transients in mangrove and wet limestone forest. Homogeneity of arthropod biomass over time was lowest in mangrove and highest in wet limestone forest (Coefficient of variation: Wet limestone – 10.3, Citrus – 24.2, Coffee – 39.1, Dry forest – 42.2, Scrub – 47.4, Mangrove – 69.4). Results from our generalized linear mixed models, as well as distance-sampling and survival models demonstrate that rainfall and food corresponded with many of the intrinsic indicators of quality (Table 3.1).

Intrinsic redstart indicators of suitability

Transients – Individual age, sex, mid-winter food availability, and early winter monthly rainfall predicted variation in the proportions of transients (Table 3.1). While neither habitat nor region was a significant predictor, differences in environmental

conditions (rainfall) drove strong variation among both habitats and regions (Figure 3.4). Highest proportions of transients occurred in the coastal region (mangrove and scrub habitats), comprising up to 50% of captured individuals in some years (Figure 3.4). Inland habitats had few transients annually with the highest documented number in 2012 (5 individuals). This regional pattern of transience corresponded with differences in winter rainfall.

Sex and Age ratio – Habitat type, total winter rainfall, and mid-winter food availability were significant predictors of sex ratios (Table 3.1). Wet limestone forest consistently had the highest ratio of males, followed by mangrove (Figure 3.5A). Dry scrub and citrus were female-dominated in all years of the study, corresponding to typically lower food availability and lower rainfall (or moisture) within their respective region.

Contrasting with sex, age ratios differed significantly over time, but not among habitats (Table 3.1). Annual shifts in population-level age ratios were experienced in all habitats. Specifically, in 2011, a major influx of young birds shifted age ratios among all habitats (Figure 3.3B), but ratios settled back to ‘normal’ levels in 2012. However, important spatial variation in age structure did occur among habitats with older birds dominating in wet limestone and older females in dry scrub (Figure 3.5B). Citrus tended to have the highest ratio of young females and mangrove of young males. Again, time was the only significant predictor of the ratio of dominant individuals (adult males), but wet limestone consistently had the highest ratio of adult males, followed by mangrove (Figure 3.5C).

Departure schedules – Habitat was the best predictor of departure timing, followed by late winter rainfall, mid-winter food, and sex (Table 3.1). Redstart males and females departed wet limestone habitat earlier than mangrove, scrub or citrus (Figure 3.6), which corresponded to highest winter rainfall and food availability. The latest overall departure times occurred in dry scrub for males and in citrus for females. Departure times for mangrove individuals fell intermediate to these wet limestone forest and scrub populations.

Annual apparent survival – Top CJS models ($\Delta AIC < 2$) of annual apparent survival for territorial individuals included region, habitat, and early winter rainfall covariates of survival (Φ), as well as time, sex and age recapture (p) covariates (Table 3.2). Model-averaged estimates showed consistently higher survival in the inland compared to coastal region (Table 3.3), consistent with higher rainfall in the inland region. The 95% confidence intervals overlapped slightly among most regions, which we attribute to relatively small sample sizes.

Density and habitat suitability

Estimates derived from the top distance-sampling models for each habitat indicate significant differences among habitats (Figure 3.7), with averages ranging from 6-16 individuals per hectare. These total density estimates in mangrove and dry scrub habitats were significantly higher than coffee, citrus, and wet limestone habitats in most years. Correspondingly, mean estimates of territorial density also indicate significant variation among some habitats over time (Figure 3.7). Density corresponded to extrinsic environmental conditions with highest density estimates in habitats with lowest mean winter rainfall, i.e. coastal scrub and mangrove.

Habitat, year, mean arthropod biomass and late winter rainfall were covariates in the top distance-sampling model ($\Delta AIC < 2$) of density (birds/ha) for the combined dataset of all habitats and all years (Table 3.4). Model selection results for habitat-specific models are consistent with these summary models, indicating that food, rainfall, and time were the most important covariates of density (Table 3.5). As a result, density estimates corresponded with regional (inland vs. coastal) variation in intrinsic indicators of habitat suitability, redstart survival and proportions of transients. Inland habitats had higher redstart survival (Table 3.3), lower proportions of transients (Figure 3.4), and lower densities, corresponding with greater rainfall in both inland habitats (wet limestone and citrus) relative to the coastal region. However, sex ratios (Figure 3.5A) and departure times (Figure 3.6) varied locally among neighboring habitats within a given region (inland – wet limestone vs. citrus; coastal – mangrove vs. dry scrub), consistent with differences in both food availability and rainfall/moisture levels. Thus density did not correspond with these intrinsic indicators of habitat suitability for redstarts. Lack of appropriate data limited how accurately we could rank coffee and dry limestone forest, but density, food, and rainfall variables placed dry forest intermediate to mangrove and scrub and coffee intermediate among inland habitats.

TABLES

Table 3.1. Results of significance tests (ANOVA) for predictor variables in top generalized linear mixed models (GzLMM) for each response variable. Mangrove, wet limestone, citrus, and dry scrub habitats included for these analyses, as well as a region (coastal and inland).

Response variable	Predictors^a	DF	X2-Value	Pr (<Chi)
Sex ratio	Habitat	3	34.4	0.000
	TotalWintRain	1	5.9	0.015
	ArthBiomass1	1	6.1	0.014
ASY Male	Year	2	22.9	0.000
Age ratio	Year	2	26.2	0.000
Transients	Age	1	7.9	0.005
	Sex	1	16.9	0.000
	ArthBiomass1	1	13.6	0.000
	EarlyMeanRain	3	11.0	0.000
Departures	Habitat	3	47.3	0.000
	ArthBiomass1	1	10.8	0.001
	Sex	1	10.6	0.001
	LateMeanRain	1	14.6	0.000

^aArthBiomass1 represents mean arthropod biomass (corrected for vegetation profiles) in early (1) and late (2) winter respectively. 'TotalWintRain' is the total rainfall (mm) from Oct-Jan for a given winter and Late Mean Rain denotes the mean rainfall (mm) from Jan-Mar for a given year. Interaction terms denoted by ':' between variables.

Table 3.2. Models of annual apparent survival (ϕ) and recapture probability (ρ) for redstarts overwintering in four Jamaican habitats (mangrove, wet limestone, citrus, and scrub)

Model ^b	K	AICc	Δ_i	w _i
$\phi_{\text{Region}} \rho_{\text{time+Sex+Age}}$	8	745.4	0	0.76
$\phi_{\text{Habitat}} \rho_{\text{time+Sex+Age}}$	10	748.7	3.4	0.14
$\phi_{\text{Region+Habitat}} \rho_{\text{time+Sex+Age}}$	11	750.8	5.5	0.05
$\phi_{\text{Region+Habitat+Rainfall}} \rho_{\text{time+Sex+Age}}$	12	752.0	6.7	0.03
$\phi_{\text{Rainfall}} \rho_{\text{time+Sex+Age}}$	8	754.6	9.2	0.01
$\phi_{\text{Null}} \rho_{\text{time+Sex+Age}}$	7	754.6	9.2	0.01
$\phi_{\text{Sex}} \rho_{\text{time+Sex+Age}}$	8	756.6	11.3	0.00
$\phi_{\text{Age}} \rho_{\text{time+Sex+Age}}$	8	756.7	11.3	0.00
$\phi_{\text{Time}} \rho_{\text{time+Sex+Age}}$	10	758.9	13.2	0.00
^a Time, sex, and age identified as top covariate for recapture probability through model-selection process.				
^b Key: K, number of estimable parameters; Δ_i , AIC _c deviance; w _i , AIC _s weights.				

Table 3.3. Estimates of annual apparent survival and profile likelihood 95% confidence intervals for redstarts overwintering in Jamaica.

Region/Habitat	Annual Apparent Survival (ϕ)	95% CIs
Inland	0.57	0.39-0.52
Coastal	0.4	0.34-0.46
Mangrove	0.4	0.34-0.46
Dry Scrub	0.39	0.33-0.46
Wet limestone forest	0.56	0.46-0.65
Citrus grove	0.57	0.45-0.68

Table 3.4. Distance-sampling models incorporating food and climatic covariate data for 2010-2012 dataset.

Model^a	K	AIC	Delta AIC	AIC weight
$\lambda(\text{Hab}+\text{Yr}) \sigma(\text{Hab})$	15	4378	0	0.63
$\lambda(\text{Hab}+\text{Food}+\text{Rain1}+\text{Yr}) \sigma(\text{Hab})$	17	4380	1.08	0.37
$\lambda(\text{Hab}+\text{Yr}) \sigma(.)$	10	4397	18.64	0.00
$\lambda(\text{Food}+\text{Rain1}+\text{Yr}) \sigma(\text{Hab})$	12	4403	24.42	0.00
$\lambda(\text{Hab}) \sigma(\text{Hab})$	13	4439	61.1	0.00
$\lambda(\text{Hab}) \sigma(.)$	8	4458	79.7	0.00
$\lambda(\text{Food}+\text{Rain1}+\text{Yr}) \sigma(.)$	7	4463	84.1	0.00
$\lambda(.) \sigma(\text{Hab})$	8	4480	101.2	0.00
$\lambda(\text{Year}) \sigma(.)$	5	4501	122.5	0.00
$\lambda(\text{Food}) \sigma(.)$	4	4507	128.5	0.00
$\lambda(\text{Rain1}) \sigma(.)$	4	4555	176.2	0.00
$\lambda(\text{Rain2}) \sigma(.)$	4	4563	184.7	0.00
Null hazard-rate	3	4564	185.1	0.00
$\lambda(\text{Rain3}) \sigma(.)$	4	4566	187	0.00
Null half-normal	2	4579	201	0.00

^a Key: λ = abundance process, σ = detection process, K= # of parameters.
^b Covariates: Hab= Habitat type, Yr= Year, Food= Mean arthropod biomass, Rain1 = late mean rain, Rain2= early mean rainfall, Rain3= total winter rainfall.

Table 3.5 Distance-sampling models for individual habitats using 2010-2012 data. Mid- and late-winter samples were combined to increase sample size. Sample included to account for effects of repeat sampling within a given year, but was not a significant covariate. Top model shown for mid and late-winter based on AIC-model selection pling models, using data collected in 2010-2012.

Habitat	Best Model	K	AIC	Delta AIC	AIC weight
Mangrove	$\lambda(\text{Year}) \sigma(.)$	5	953.8	0	0.68
	$\lambda(\text{Food}+\text{Year}) \sigma(.)$	6	955.6	1.9	0.27
Wet limestone	$\lambda(\text{Year}) \sigma(.)$	5	681.6	0	0.59
	$\lambda(\text{Rain1}) \sigma(.)$	4	682.4	0.75	0.40
Scrub	$\lambda(\text{Food}) \sigma(.)$	4	576.8	0	0.45
	$\lambda(.) \sigma(.)$	3	578.6	1.73	0.19
	$\lambda(\text{Year}) \sigma(.)$	5	578.6	1.73	0.19
Citrus	$\lambda(\text{Year}) \sigma(.)$	5	683.6	0	0.8
	$\lambda(\text{Food}) \sigma(.)$	4	687.3	3.7	0.12
Coffee	$\lambda(\text{Rain1}) \sigma(.)$	3	915.7	0	0.49
	$\lambda(\text{Year}) \sigma(.)$	4	916.1	0.44	0.40
Dry limestone	$\lambda(\text{Rain1}) \sigma(.)$	3	565.2	0	0.61
	$\lambda(\text{Year}) \sigma(.)$	4	566	0.9	0.39

FIGURES

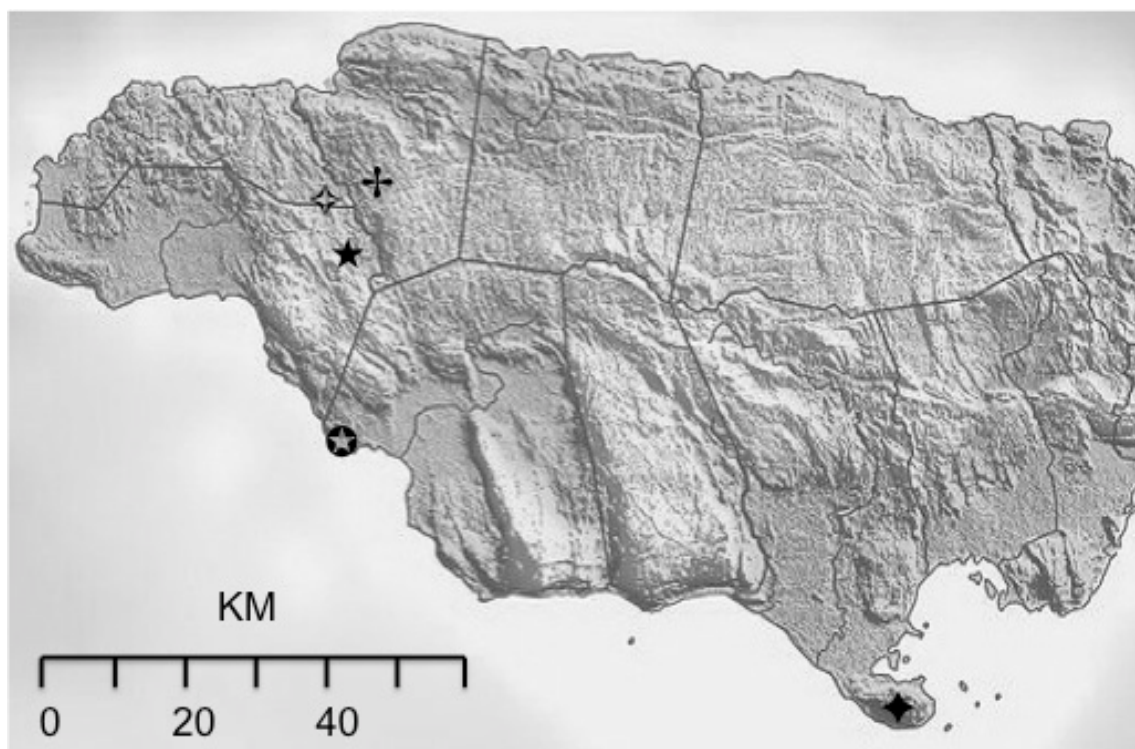


Figure 3.1. Map of research site locations in central and western Jamaica. Site key: (★) Mangrove and scrub; (★) Wet limestone; (◇) Citrus; (✚) Coffee; (◆) Dry limestone.

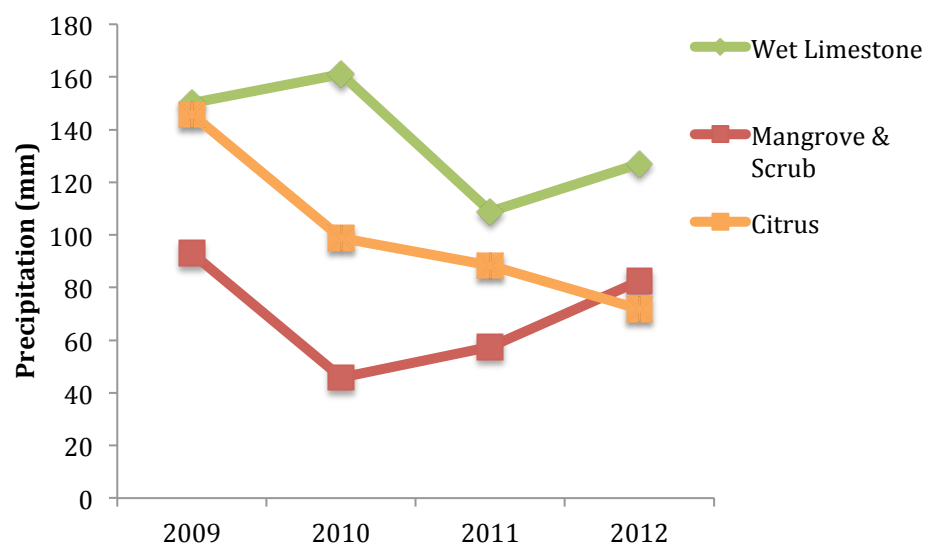


Figure 3.2 Average monthly winter rainfall (Oct-Mar) from 2009-2012 for each habitat. (Scrub and mangrove sites lie directly adjacent to one another, thus rainfall patterns are identical).

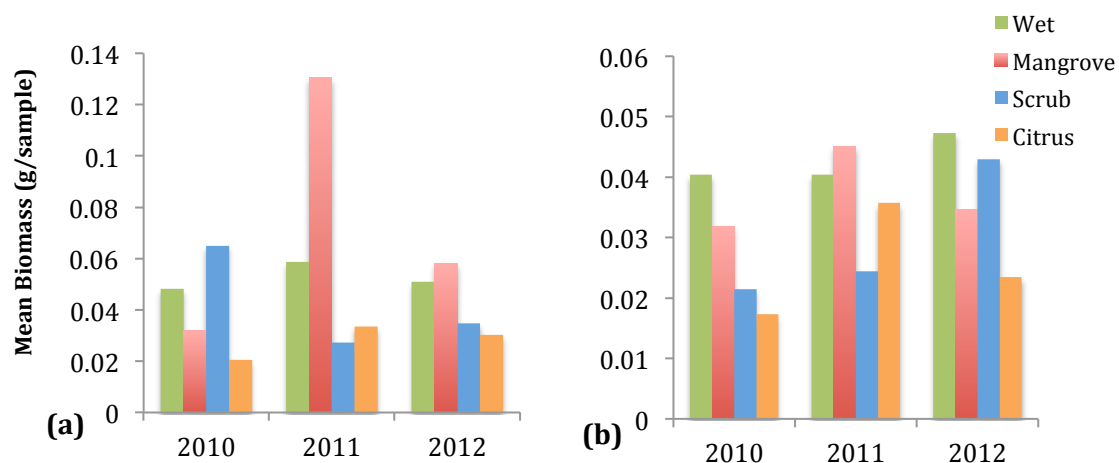


Figure 3.3 Availability of arthropods in the four core habitats from 2010-2012. Mean biomass of mid-winter (a) and early spring (b) samples shown for each habitat.

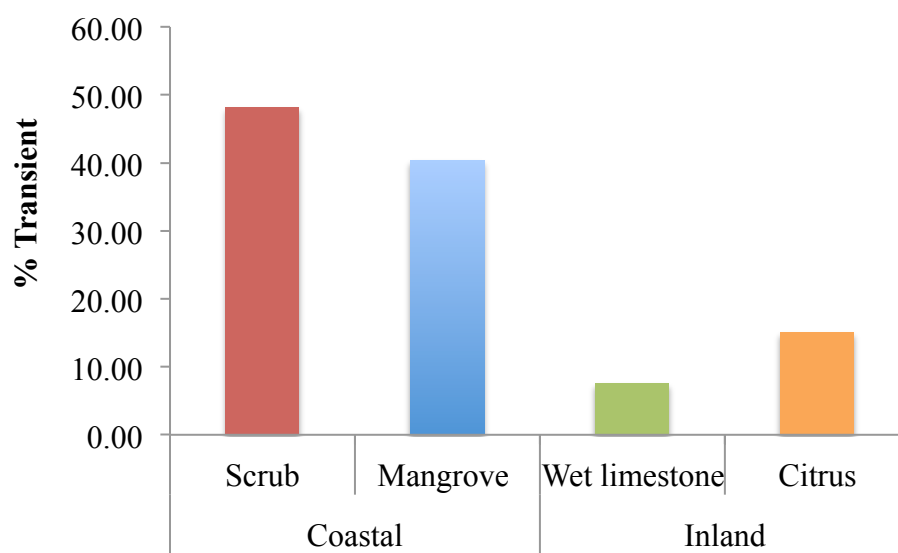


Figure 3.4. Mean proportion of transient individuals captured in each habitat that were not territorial within our research area.

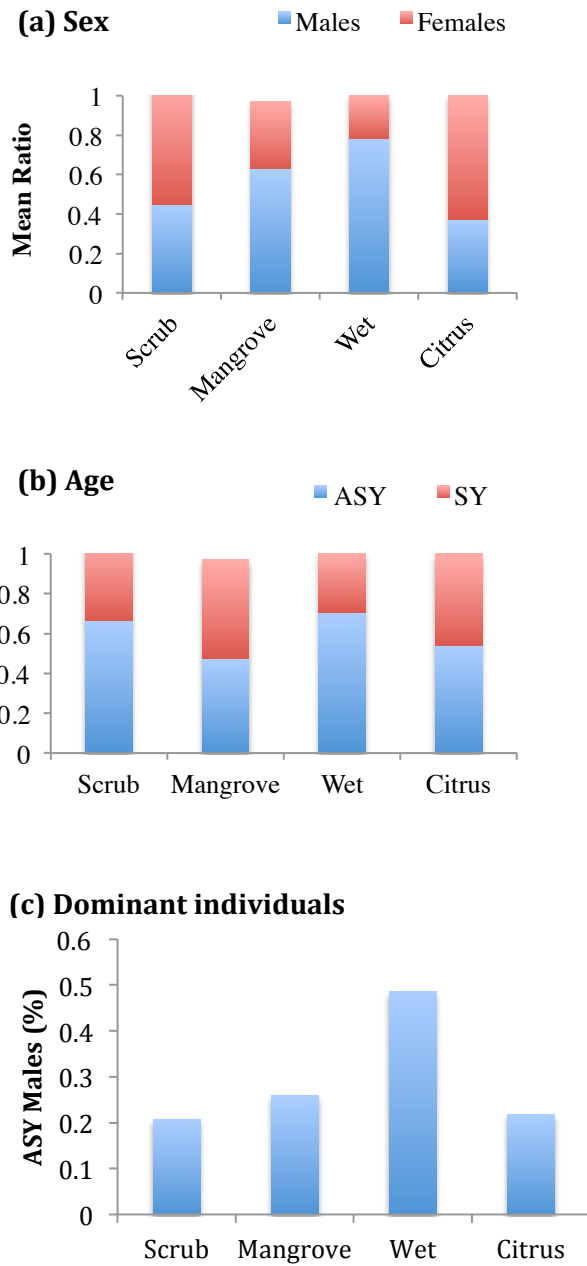


Figure 3.5 Variation in sex (a), age (b) ratios, and distributions of dominant individuals (c) among four Jamaican habitats.

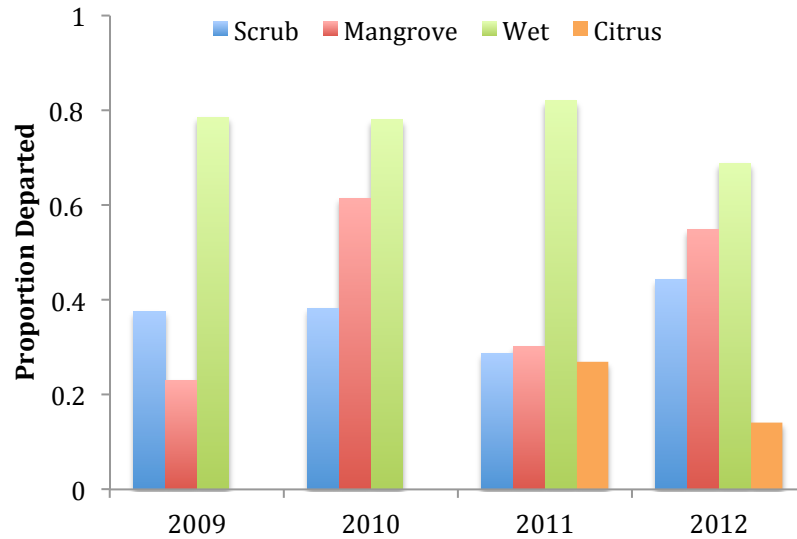


Figure 3.6 Proportion of individuals within each habitat that departed for spring migration by May 6th.

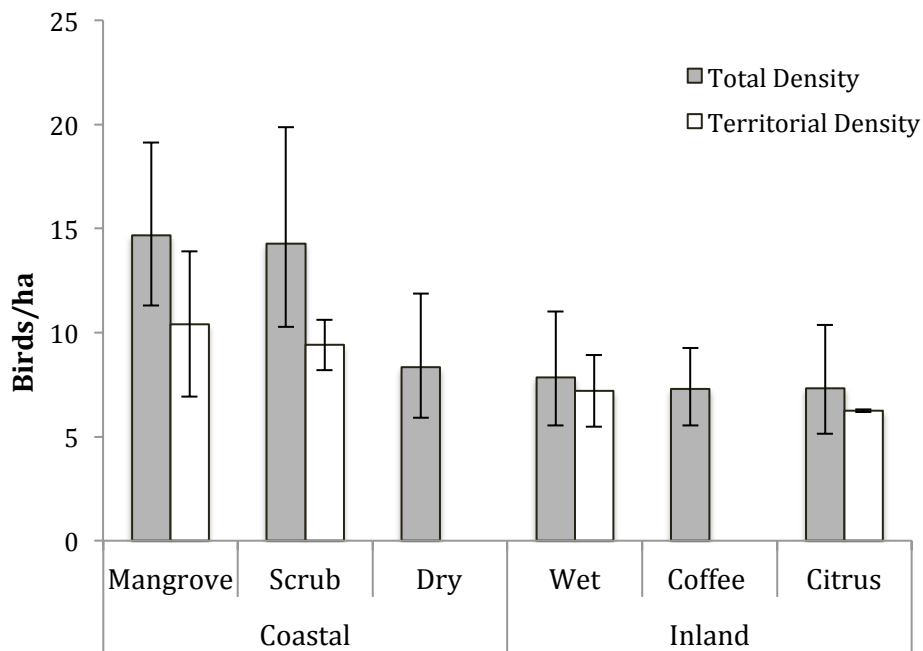


Figure 3.7 Territorial vs. total mean density by habitat. Territorial density generated from annual summary maps for each habitat (error bars: ± 1 SD). Total density, i.e. territorial plus transient individuals, was estimated from unmarked distance-sampling models (error bars: 95% confidence intervals).

DISCUSSION

Habitat quality determines the performance and survival of migratory passerines in winter (Lefebvre and Poulin 1992, Price and Gross 2005). Within territorial species, individuals appear to saturate the most suitable habitats first with dominant individuals benefitting through better performance and survival (Marra 2000, Townsend et al. 2012). Our results indicate that intrinsic indicators of habitat suitability for American redstarts vary in response to extrinsic environmental conditions to produce gradients of habitat suitability at multiple spatial scales. Transience, survival and density of redstarts suggest that variation in environmental conditions (winter rainfall) drive differences in redstart populations regionally and do not correspond with behavioral dominance patterns that typically structure populations at more local (within region) scales, i.e. more males in better habitats (Marra 2000). Between habitats within a given region, differences in sex structure, departure timing, and to a lesser extent transience reflect variation in local environmental conditions, primarily food availability. These results suggested that suitability varies at multiple spatial scales, both between and locally, between neighboring habitats.

Extrinsic environmental conditions (rainfall and food availability) varied regionally and locally and corresponded with intrinsic indicators of habitat suitability for redstarts, consistent with our first hypothesis. Between regions, lower rainfall corresponded with lower survival and more transients in the more arid coastal habitats, which highlights the potential vulnerability of this species to increasing drought or fluctuations in rainfall in the dry season (Silllett et al. 2000, Studds and Marra 2005, 2007, Pearce-Higgins 2009, Ockendon et al. 2014a). High proportions of transients in coastal

habitats with low winter rainfall indicate that spatial behavior may be influenced by environmental conditions and that this is an important intrinsic indicator for assessing the consequences of habitat suitability for wintering populations.

Previous findings among migratory passerines worldwide showed that food is a strong indicator of habitat suitability and often determines population distributions (Parrish and Sherry 1994, Lefebvre and Poulin 1996, Katti and Price 1996, Gross and Price 2000, Johnson et al. 2001, Cooper et al. 2015). In this study, primarily dominant individuals (older males) appeared to control local (within region) access to the greater food resources in wet limestone and mangrove habitats, which corresponded with relatively earlier spring departure dates (Studds and Marra 2011, Rockwell et al. 2012, Cooper et al. 2015). Individuals inferred to be socially subordinate (younger individuals, and females; Marra and Holmes 2001) were more frequent in the two habitats with later departure times (dry scrub and citrus), suggesting worse physical condition in late winter (Studds and Marra 2007). This pattern of higher-performing individuals occupying better quality habitats on a local scale is consistent in other territorial species, which are food-limited in winter and partition habitats via social dominance mechanisms (Wunderle 1995, Gross and Price 2005, Koronkiewicz and Sogge 2006, Townsend et al. 2011, Smith et al. 2011).

Importantly, while we found significant differences in habitat suitability both within and between regions, intrinsic indicators were not all congruent. Survival, transience, and density varied between regions, while spring departure dates and sex ratios varied within regions. The first set of indicators corresponded most strongly with variation in rainfall and the second with food availability. This suggested that

environmental conditions differentially affect aspects of redstart winter population dynamics and emphasizes the importance of considering a wide range of intrinsic indicators (Johnson 2007).

We found partial support for our second hypothesis that density of a territorial species like the redstart would be inversely related to suitability, i.e. highest in low quality habitats (Fretwell and Lucas 1970). In this study, low densities corresponded with a subset of intrinsic (high survival, few transients) and extrinsic (relatively higher winter rainfall) indicators, characteristic of the inland region. However, density did not correspond to local variation in sex ratios or spring departure times between neighboring habitats. From this we infer that environmental conditions such as rainfall or resource predictability may be the stronger drivers of spatial differences in redstart distribution, a pattern supported in both Neotropical and Afro-Palearctic migratory species (Wilson et al. 2011, Ockendon et al. 2014a). Density only corresponded with regional differences in environmental conditions, but was not a useful indicator of local habitat suitability. This highlights the importance of comparing density or abundance estimates with other intrinsic indicators of habitat suitability over multiple spatial scales.

Our assessment of habitat quality differs from previous work on redstarts in Jamaica, which identified coastal mangroves as the highest quality habitat, but did not include wet limestone forest (Marra and Holmes 2001, Johnson et al. 2006). Inclusion of this habitat suggested that inland habitats are more suitable for redstarts in terms of annual apparent survival and likelihood of maintaining a territory (i.e. fewer transients). Sex ratios, departure times, and food availability indicated that wet limestone forest and mangrove are the most suitable habitats within their respective regions.

Regional vs. local-level patterns of abundance

Anthropogenic and natural disturbances are regular occurrences across coastal habitats. Variation in dry season rainfall (Studds and Marra 2005), as well as logging and livestock grazing lead to regular disturbances (AMP pers. obs.). Although weather and humans affect habitats island-wide, greater disturbance along coastal areas from hurricane events (Newton 2004) may decrease the predictability and diversity of prey types, relative to wet limestone forest. Our evidence suggests that food availability is more variable in the coastal region, which may be a limiting factor for birds occupying habitats like dry scrub where resources are typically low in winter. Increased fluctuation in food from disturbances may further reduce the quality of coastal habitats and explain the high numbers of transients and low survival rates we observed. Additionally, coastal habitat vegetation is structurally simpler and lower in diversity, particularly in scrub habitats, which typically correlates with less arthropod prey diversity/abundance (Johnson and Sherry 2001, Johnson et al. 2005). The combination of greater regular disturbance and lower structural complexity may contribute to the quality differences observed between inland and coastal regions.

Rainfall and/or moisture levels also distinguished coastal from inland, montane habitats studied. On the coast, mangrove substrate remains inundated in all but the worst drought years (Studds and Marra 2007) and trees remain evergreen, while dry scrub trees typically drop leaves in the dry season (Parrish and Sherry 1994). Wet limestone forest habitats experienced the highest rainfall annually, while citrus sites consistently experience greater annual rainfall than coastal habitats and do not drop leaves during the dry season. However, pest control practices strip understory vegetation in citrus groves,

causing erosion, dryer soil conditions, and reduced foraging areas (AMP pers. obs). These local dichotomies in moisture correspond to relatively higher food availability between neighboring habitats and likely explain the greater proportions of dominant individuals in mangrove and wet limestone forest (Smith et al 2010, Wilson et al. 2013). Consistency in vegetation and/or predictability of resources throughout the dry season is linked to higher numbers of dominant individuals and site-persistence of redstarts and other migratory species (Strong and Sherry 2000, Latta and Faaborg 2002, Gordo et al. 2007, Both et al. 2010, Smith et al. 2011, Toms 2011). Wet limestone and mangrove represent the most stable habitats in their respective regions, while regional differences in rainfall likely make inland areas the most reliable region.

Conservation implications

Our results suggest that the inland region and wet limestone habitat in particular are most suitable for overwintering American redstarts in Jamaica, which provides new insight for a species so tightly associated with coastal habitats by past research efforts (Marra 2000, Studds and Marra 2005, Tonra et al. 2011). These studies emphasized the importance of conserving the little remaining coastal mangroves (Sherry and Holmes 1996, Marra and Holmes 2001), but results of the present study suggest that interior, wetter forests also deserve increased attention. Wet limestone forest habitat is extremely threatened by a variety of anthropogenic pressures and is also where many endemic Jamaican species occur, many of which also face population threats. In western Jamaica, timber is one of the few remaining profitable natural resources, and agricultural deforestation is prevalent in poor rural communities (Eyre 1986, Weis 2000, Chai et al.

2009, Newman et al. 2014), while intensive mining in central and eastern Jamaica have led to extensive forest loss (Evelyn and Camirand 2003, Kennedy and Marra 2010). Additionally, residential expansion into forested areas adjacent to urban centers has led to further habitat loss and fragmentation (Eyre 1979). Most remaining wet limestone forest is found on steep, isolated hillsides where crop production is difficult, but such constraints will not stand up to the expansion of agriculture and logging development forever. Conservation effort is needed not only for coastal mangroves but also for remaining patches of wet forest in Jamaica's interior, especially to buffer both migrant and resident populations from forecast anthropogenic drought (Meir and Pennington 2011).

Additionally, our findings support the suitability of some agricultural habitats for wintering migrant species, particularly when closely associated with areas of wet forest (Jirinec et al. 2011). Given the ecosystem services of migratory birds, e.g. in pest control (Johnson et al. 2009, 2010), conservation efforts should focus on working with farmers to protect forest fragments associated with agricultural areas from timber harvest and other exploitation.

Chapter Four

Buffer and crowding effects act at different spatial scales to regulate a long-distance migratory bird population during the non-breeding season

ABSTRACT

Changes in population density can regulate populations at multiple scales. Within habitats, this occurs via competitive behavioral interactions that result in crowding effects with consequences for individual condition and survival. Among habitats, a buffer effect can create interactions between density and habitat quality. As density increases, individuals are forced into poorer quality habitats and more individuals are forced into a transient behavioral strategy, which regulates populations via negative feedback on demographic rates. Few studies have assessed demographic consequences of changing density in animal populations during the non-breeding season. This study tested for crowding and buffer effects on annual apparent survival, spring departure timing (potential carry-over effect), and spatial behavior (transience) of American Redstarts (*Setophaga ruticilla*) overwintering in diverse non-breeding habitats in both coastal and inland regions of Jamaica. As overall population size increased, redstart density did not vary or increase disproportionately in low quality habitat, contrary to buffer effect predictions. However, proportions of transients increased with concurrent population increases in the poor quality coastal region, suggesting a regional buffer effect. Survival

did not change over time, but was significantly lower in the coastal region. Within this coastal region, transient proportions were highest and spring departure latest in the poorest habitat, dry scrub. These demographic responses corresponded to both increasing population size and declining food availability, consistent with a local (within-region) buffer effect and increased food competition via crowding. In the inland region, demography did not change with increasing population size in high quality wet limestone forest, suggesting individuals are relatively shielded from fluctuations in density by ecological conditions (greater rainfall and food availability). Overall, we find that a buffer effect can impact both regional and local demographic responses to changing population size and can lead to crowding effects in poorer habitats.

INTRODUCTION

Animal populations are limited both by extrinsic environmental and intrinsic behavioral mechanisms, but how these processes operate in free-living animals remain poorly understood for most species (Murdoch 1994, Turchin 1999). Extrinsic environmental factors like rainfall limit population abundance via resources such as food (Newton 2004) and habitat. Intrinsic factors can create density-dependent, regulatory feedback on population size (Hixon et al. 2002), e.g. when a denser population intensifies competition for limited resources (Sutherland 1996, Lariviere and Messier 1998, Ferrer et al. 2014, Grunkorn et al. 2014). Increased competition can reduce physical condition, reproductive success, or survival, causing a decline in abundance. However, few studies have assessed densities among multiple habitats simultaneously with indicators of individual condition and survival to assess such mechanisms in wild populations (but see

Ferrer and Donazar 1996, Gill et al. 2001, Gunnarsson et al. 2005). Understanding how extrinsic environmental factors like weather, habitat and resource availability interact with intrinsic behavioral mechanisms is critical for predicting population responses to environmental disturbances such as climate change and habitat degradation (Sillett et al. 2000, Sutherland and Norris 2002, Reed et al. 2014).

The buffer effect was one of the earliest intrinsic regulatory mechanisms proposed. It predicts that the variance in individual density among habitats differs, being greatest in the ecologically least buffered (lowest quality) habitats (Kluyver and Tinbergen 1953, Brown 1969). Brown (1969) predicted that the buffer effect would occur in two stages: 1) more individuals pushed into poorer habitats and 2) subsequently more individuals would be forced out a territorial strategy entirely and become transients. Much research has demonstrated that proportions of individuals occupying low quality habitats will increase more than in high quality sites when population size increases (Gill et al. 2001, Soutullo et al. 2006, Sullivan et al. 2015). However, no recent studies have assessed the second component of Brown's theory and assessed the relationship between transience and a buffer effect mechanism of population regulation.

As density increases within habitats, behavioral interactions between individuals can cause density-dependent negative feedback via crowding (Begon et al. 1996, Rodenhouse et al. 1997, Sillett et al. 2004, McKellar et al. 2014). Crowding within habitats can also act through despotism to push individuals into less suitable habitats consistent with a buffer effect. When population size is high and availability of resource-rich habitats low, this competitive mechanism can also lead to saturation of high quality habitats and floating or transient behavior among otherwise territorial populations

(Fretwell 1972, Kokko and Sutherland 1998). Changes in population size can thus lead to both changes within habitat density (“crowding effects”; Rodenhouse et al. 1997) and among habitats such as predicted by the buffer effect, and these are not mutually exclusive regulatory mechanisms.

Population regulation has been documented in many breeding populations of migratory birds (Newton 2004, Sillett and Holmes 2005, Dhondt 2011). As densities increase, vital rates such as survival and fecundity decline as a result of crowding or buffer effects (Rodenhouse et al. 2003, Sillett et al. 2004, Gunnarsson et al. 2005, Soutullo et al. 2006, Nevoux et al. 2011). However, few studies have assessed these mechanisms during the non-breeding season. Gill et al. (2001) demonstrated that as population size in Black-tailed Godwits (*Limosa limosa*) increased, subordinate individuals occupied poorer quality habitats, resulting in lower annual survival and later spring departure dates. Non-breeding sanderlings (*Calidris alba*) increasingly occupied poor quality sites as population size increased among African wintering habitats (Ntiemoa-Baidu et al. 2014). Finally, American redstarts (*Setophaga ruticilla*), a long-distance migratory songbird wintering in the Neotropics (Marra et al. in review), declined in body condition and survival with density, but only one of two adjacent habitats. To our knowledge, no studies have tested for a buffer effect or looked for its potential consequences in a migratory songbird during the non-breeding season. Furthermore, no studies have assessed the impact of a buffer and crowding effect on the space-use behavior of a typically territorial species.

In years of low resource availability and/or high population size, the benefits of territoriality can decline to the extent that a transient strategy becomes beneficial (Petit et

al. 1995, Kokko and Sutherland 1998). More transients may thus occur in habitats of lower suitability, e.g. fewer resources, with overall population size. Alternatively, increases in abundance may saturate habitats to the extent that space limitation forces individuals into a transient strategy through territory exclusion, regardless of the demographic costs or benefits (Brown and Long 2007, Lenda et al. 2012). In either scenario, transience should correspond with differences in density over space or time if a buffer effect is operating. What remains poorly understood is how these individuals may be affected by regulatory mechanisms like the buffer effect, and what extrinsic ecological circumstances favor transience. Brown (1969) proposed that increases in the numbers of transients are the natural consequence of buffer effects on habitat occupancy, but no studies have subsequently tested density-dependent effects on transience. Moreover, insofar as greater population density contributes to declining resources, particularly in poor habitats, within-habitat density should contribute to negative demographic rates and greater degree of transience, i.e. crowding effects can exacerbate buffer effects: Not only are the two not mutually exclusive, but they probably also interact. However, to our knowledge no study has tested for both effects simultaneously, an important goal in understanding buffer effect mechanisms.

Our study focused on buffer and crowding effects in a well-studied migratory passerine, the American Redstart (*Setophaga ruticilla*) on its non-breeding grounds. Gradients of habitat suitability are known, characterized by variable food and rainfall among diverse wintering habitats (Sherry and Holmes 1996, Marra and Holmes 2001, Johnson et al. 2006) and in two regions differing in rainfall (Studds and Marra 2007, Peele et al. in prep- hereafter Chapter 2). Based on these habitat gradients both locally

and regionally, we tested buffer and crowding effects, using three independent means. We predicted that (1) in high-abundance years, the redstart population shifts toward proportionately greater use, higher density, and greater density variance in relatively poor habitats, consistent with a buffer effect. If both buffer and crowding effects are operating, we predicted (2) density-dependent increases to proportions of transients and (3) decreased demographic success (later spring departure date, reduced survival) in response to increased density. Finally, (4) food availability should respond to increased densities within habitats, demonstrating the effects of competition (crowding effects).

METHODS

Study species—American redstarts (*Setophaga ruticilla*) are ideally suited for assessing density-dependent mechanisms for several reasons including occupation of a range of habitat types (Sliwa and Sherry 1992, Johnson et al. 2006) and fluctuating densities in Jamaican winter habitats (Marra et al. in review). Additionally, social dominance mechanisms are also known to affect the distribution of individuals locally (Marra et al. 1993, Marra 2000) and regionally (Sliwa and Sherry 1992), allowing us to make informed predictions about individuals' responses to changing abundances at local and regional spatial scales. Finally, redstarts are aerial insectivores (Sherry and Holmes 1997), which informs focused arthropod sampling efforts.

Habitats—We selected six habitats from two distinct regions in Jamaica, the southern coast and inland, mid-elevation mountains. Within each region, we chose the three most prevalent ecotypes. Coastal habitats were mangrove, dry scrub, and dry limestone forest;

inland habitats were two types of orchard (coffee, citrus) and wet limestone forest (see Peele et al. Ch. 3 for map and detailed habitat descriptions). Bird density and environmental data (e.g. rainfall and food) were collected from all six habitats, and demographic data from two habitats per region: mangrove and scrub, and citrus and wet limestone forest. These habitats include not only widespread habitat types, but also a range of human disturbances from relatively undisturbed wet limestone forest to agriculture, an array of conditions probably typical of most wintering regions for redstarts.

Field methods—Fieldwork extended from early January through early May 2009-2013. We collected data on rainfall and all demographic variables from 2009-2012 and a final year of survival and rainfall data in 2013. Arthropod (food) data were collected from 2010-2012 (field data collection described in detail in Peele et al., Chapter 3).

To estimate *total* density in each habitat, i.e. density of all individuals regardless of spatial behavior, we distributed 20 point-count locations in each of the six habitats with the exception of scrub, which had 15 sites. We used distance-sampling survey protocols (Buckland et al. 2001), sampling each point in mid- and late winter (early-mid February and late March-early April). By mid-winter, territories are established and individuals usually persist until departure for spring migration (Marra et al. 1998, Marra 2000). One experienced observer (AMP) carried out these surveys in all years, along with one new observer each year trained by AMP to recognize species-specific winter vocalizations.

We used a single observer per sample point to record all redstarts detected, age and sex if possible, type of detection (seen/heard), and estimated distance (m) from observer for each individual bird within a ten-minute survey period. We classified birds detected at >50m as outside the survey boundaries, due to difficulty of redstart chip note identification beyond this range (AMP pers. obs.).

Research plots of ~5-6 ha were set up in each habitat and flagged with a grid every 50m to allow accurate mapping of location. We used passive and individual (bird)-targeted mist netting methods annually to capture and band as many territorial birds as possible, from mid-January to late March. We used unique combinations of one aluminum and two color bands to distinguish individuals once released. We re-sighted and mapped territories from mid-January to early April, and generated summary maps for estimating territorial density per habitat.

Marked methods on each of the four intensive study habitats (mangrove, dry scrub, wet limestone forest, and citrus grove) (1) allowed estimating the proportion of transients, (2) timing of spring departure, and (3) annual survival. We estimated the number of transient individuals as the difference between estimated total densities of individuals (using distance-sampling) compared to estimated number of territorial individuals from seasonal summary maps (see Chapter 2 for detailed methods). We used summary maps to monitor departure timing from April 15 to 2nd week of May, which limited this parameter to territorial individuals. We visited each individual's territory every three days in mangrove and scrub sites to confirm presence or absence of marked redstarts. Due to person constraints, we only visited citrus territories every other day, but believe this did not bias results given the relative ease of detection and identification of

banded individuals in this habitat (see Chapter 3, Studds and Marra 2005, Cooper et al. in press for further details of departure field methods). We calculated the proportion of the population departed from each habitat by May 6th for subsequent comparison among habitats. We generated estimates of annual apparent survival using mark-recapture data that generated individual records of occurrence annually, and did so for both territorial and transient individuals where possible.

We used sweep netting to sample arthropod biomass at each point-count location in mid (early February) and late winter (late March-early April) from 2010-2012 (also described in Chapter 3, Cooper et al. 2012). The same person collected samples every year to avoid individual bias (Cooper et al. 2012). Additionally, we took measurements of foliage height profiles at each point-count location, which we used to generate an index of vegetation volume for each habitat (Chapter 3). This index was used to correct arthropod biomass samples for differences in vegetation volume, assuming constant densities per foliage volume with height above ground. Meteorological Service weather stations within 5km of each field site provided daily precipitation logs to generate mean monthly rainfall data for each habitat. We focused on the winter months of October-March, estimating early winter mean (Oct-Dec), late winter mean (Jan-Mar), and total winter mean rainfall to use as covariates in later analyses.

Statistical methods—Using hierarchical distance sampling methods (Royle et al. 2004), we estimated population density from point-count survey data in all six of our study habitats (See Chandler 2011, Sillett et al. 2012, and Chapter 2). Since density differs by habitat (Chapter 3), we fit separate models to each habitat including a set of environmental

covariates (early, late, and total winter mean rainfall, arthropod biomass). Using AIC model-selection methods, we identified the top model for each habitat ($\Delta\text{AIC} < 2$) and assessed fit using a chi-squared test. We estimated density for each habitat from top models ($\Delta\text{AIC} < 2$) and classified this as our best estimate of total density, including territorial, transient, and any other kinds of individuals. We estimated total population abundance estimate for each habitat and year. Additionally, we estimated density of territorial individuals from summary territory maps, generated from mapping data collected from mid-January through late March each year in our four intensive study sites (wet limestone, citrus, mangrove, and dry scrub; Chapter 2). In subsequent analyses and comparisons, we tested the effects of both *total* and *territorial* density.

We used an analysis of covariance (ANCOVA) to assess changes in density among all study habitats over time to test the buffer effect, specifically whether slopes of density versus time (year) differed among habitats,. We used habitat-specific density as the response variable, habitat as the categorical factor, and overall population size (all habitats pooled) as the continuous covariate. We compared slopes among habitats to assess differences in the rate of increase among habitats. Additionally, we calculated the coefficient of variation (%) of density per habitat to compare variability. Using linear regression, we also assessed how the proportion of territorial and total (territorial + transient) individuals per habitat changed as a function of overall population size.

To identify relationships between proportions of transients and a set of predictor variables (habitat, region, density, food availability and winter rainfall) we used generalized linear mixed models with random effects. Food data were only available for 2010-2012, thus we analyzed just these years of data to compare food and density effects.

We then analyzed the 2009-2012 data minus the food predictor variable to assess effects of density using a larger sample size. Earlier results (Chapter 3) indicated that transience and departure are likely affected by age and sex of individuals, so we included these as predictor variables. We also tested for the two-way interactions of density with other response variables including region, habitat, food and rainfall, where possible (we could not address a habitat x density interaction for transient models, given sample size constraints). To account for repeat measurements of some, but not all individual birds in multiple years, we also included a random effect of individual in our models. We used AIC and r-squared values to rank models, and an iterative approach to test the significance of predictor variables in the top models for each response variable. We used these same methods to assess the relationship between departure timing and density. All analyses were carried out in program R (R Core Team, 2013).

To estimate annual apparent survival we used Cormack-Jolly-Seber models (Lebreton et al. 1992), using the package rMark (Laake 2013) in program R (version 0.981102). We followed the hierarchical approach used by Peele et al. (Chapter 3, Wilson et al. 2012), first generating models of recapture (p) using age, sex, habitat, and time as covariates. We used AIC model selection to identify the best model for recapture rate, and kept this constant for all subsequent models. We then repeated this process with models of survival (ϕ), including early winter rainfall, food availability, and annual territorial and total density (birds/ha) as covariates. We included additive and interaction effects among density, habitat, and region covariates, but we found no important interactions. We know from previous work (Chapter 3) that food availability was not a significant predictor of survival ($AIC_c > 2$), thus we excluded food. We ranked models

based on Akaike's information criterion (AICc) and associated likelihood with AICc weights (w_i ; Burnham and Anderson 2002). Finally, we used model averaging across all models to generate annual apparent survival estimates by region, habitat, and density, i.e. the top three models. We used the same process to estimate survival of transient individuals from mangrove and scrub habitats, where sample sizes were sufficient. We consider these latter (transient) estimates return rates, rather than apparent survival probabilities, given that high redstart site fidelity is less likely and permanent emigration more probable with transient individuals.

Changes in food availability are dependent on both extrinsic environmental conditions and numbers of individual consumers using the resource, especially when renewal rates are low. Thus, to evaluate crowding effects, we calculated food availability (g) per individual bird in late winter, and used a multivariate linear regression with bird density as the independent variable. We used a Shapiro-Wilkes test to assess the normality of the food dataset. Annual winter rainfall and habitat type were included as predictors of food availability. We assessed model weight and significance using r -squared and p -values. Finally, we used an analysis of variance (ANOVA) to test the significance of each covariate in the model with the greatest weight.

RESULTS

Changes in density

Densities of redstarts varied significantly among habitats over the four years of study (F-value: 72.8, $F_{DF: 1}$, $p < 0.001$; Figure 4.1). Both the proportion and mean density of individuals occupying all three higher quality inland habitats were consistently lower

than in coastal habitats, indicating significant regional differences in redstart distributions. In response to annual increases in total population size from 2009-2011, rate of change in within-habitat density was similar among all habitats (F-value: 1.5, F_{DF} : 5, p : 0.25). There was no change in the proportions of individuals occupying coastal (r^2 : 0.18, p : 0.57) and inland (r^2 : 0.18, p : 0.55) regions as population size increased. Additionally, change in the proportion of territorial (Figure 4.2A, 4.2B) and total (territorial + transient; Figure 4.2C, 4.2D) individuals occupying each habitat did not vary significantly as population size increased.

Additionally, variance in local density (CV) by habitat among years was ranked (highest to lowest habitat) citrus = 50, dry limestone 46, wet limestone 45, scrub 35, mangrove 39, and coffee 22. The variance of territorial densities showed a similar pattern for the three habitats for which data were available (wet limestone 24, mangrove 20.1, and scrub 17.1).

Effects of density on transience, spring departure, and survival

Proportions of transient individuals varied by early winter rainfall, year, sex, age, and habitat-specific territory density (Table 4.1). It was surprising that these variables outweighed the effects of habitat and region on transient occurrence, but early winter rainfall was less surprising considering how much it varied by region (Figure 4.3). The 2010-2012 data subset included food availability as an additional predictor and in the best model, proportions of transients varied by mid-winter rainfall, food, and habitat. Transient proportions were greatest in coastal habitats (Figure 4.4), where densities were high. Within this region, scrub populations maintained consistently higher proportions of transients than mangrove, and these were positively correlated with overall population

size in both mangrove (r^2 : 0.92, p : 0.44) and scrub (r^2 : 0.59, p : 0.82). Among inland habitats, numbers of transients were relatively low (Fig 4.4).

Spring departure patterns varied by habitat, sex, early winter rainfall, and territorial density from 2009-2012 (Table 4.1, Figure 4.5). For the 2010-2012 data subset, late winter rainfall, sex, and habitat determined the proportion of territorial individuals that departed for spring migration by 6th May. Within the coastal region, individuals in mangrove tended to depart earlier than neighboring scrub birds, but later than wet limestone forest occupants (Figure 4.5). Among inland habitats, wet limestone birds departed earlier than citrus, which had the latest departure times of all habitats.

Total density (territorial plus transient) and region predicted annual apparent survival of territorial individuals (Table 4.2). Survival declined with total density and varied by habitat (Table 4.3), but regional effects were more pronounced. It is important to note that total density was a stronger predictor of survival than territorial density. Annual apparent survival was consistently highest in wet limestone forest and citrus, lowest in mangrove and scrub habitats. Total density predicted annual survival (or return rate) for transient individuals (High density ϕ : 0.37, SE: 0.06, CI: 0.26-0.49; low density ϕ : 0.33, SE: 0.07, CI: 0.22-0.48), indicating no differences among the mangrove and scrub birds using this spatial strategy (too few transients occurred in inland habitats to estimate this parameter there).

Food availability and rainfall-

Food availability (arthropod biomass (g)/bird) varied by habitat type (r^2 : 0.60, F -value: 3.62, F_{DF} : 5, p : 0.03). Coastal habitats had lower food availability than inland wet

limestone forest in most years (Figure 4.6), indicating the effects of high density and habitat quality on arthropod biomass. Low suitability habitats experienced the greatest decline in food, as densities increased from 2009-2011. This negative effect of increasing density on food availability in mangrove in 2011 was only offset by a concurrently greater increase in arthropod biomass, unrelated to rainfall. This was the only habitat in which an increase in redstart density corresponded to a temporary increase in food availability. Comparing inland habitats, citrus had consistently lower annual food availability per individual than wet limestone. Early winter rainfall patterns were correlated with differences in food availability (r^2 : 0.3, F-value: 6, F_{DF} : 1, p : 0.03). Wet limestone forest received the greatest winter rainfall annually, followed by citrus and coffee (Figure 4.3). Coastal habitats typically experience a stronger drought in mid to late winter, which was especially intense from 2009-2011, averaging only 23 mm per month. Overall, food was negatively affected by increasing populations and rainfall, particularly in low suitability coastal scrub habitat where high redstart densities combined with drought conditions resulted in the consistently lowest food availability (Fig. 4.6).

TABLES

Table 4.1 Generalized linear mixed model results for transience, departure, and age responses variables. Sample years indicate that data subset used for the different models. The 2010-2012 subset includes food effects. Predictors^a indicate independent variables of top model for each response variable (based on AIC values).

Sample Years	Response	Predictor	X ²	DF	Pr
2009-2012	Transience	Early Rain	53.1	1	<0.001
		Year	52.2	3	<0.001
		Sex	18.5	1	<0.001
		Age	8.5	1	0.004
		Terr Dens	5.1	1	0.024
	Departure	Habitat	74.2	3	<0.001
		Sex	44.2	2	<0.001
		Early Rain	20.4	1	<0.001
		Terr Dens	3.7	1	0.050
2010-2012	Transience	Habitat	73.1	3	<0.001
		Early Rain	14.9	1	<0.001
		Mid Food	11.1	1	0.001
	Departure	Habitat	47.3	3	<0.001
		LateRain	14.6	1	<0.001
		MidFood	10.8	1	0.001
		Sex	10.6	1	0.001

^a Key: X², Chi-squared value; DF, degrees of freedom; Pr, p-value.

^b TerrDens, territorial density; EarlyRain, mean precipitation from Oct-Dec; LateRain, mean precipitation from Jan-Mar; MidFood, arthropod biomass sampled in early Feb.

Table 4.2 Models of survival (ϕ) and recapture (p)^a for redstarts overwintering in four Jamaican habitats.

Model^b	K	AICc	Δ_i	wi
$\phi_{\text{Region Ptime+Sex+Age}}$	8	745.4	0	0.52
$\phi_{\text{Total Density+ Region Ptime+Sex+Age}}$	9	747.4	2.0	0.19
$\phi_{\text{Habitat Ptime+Sex+Age}}$	10	748.7	3.4	0.09
$\phi_{\text{Total Density*Region Ptime+Sex+Age}}$	10	749.4	4.1	0.07
$\phi_{\text{Total Density Ptime+Sex+Age}}$	8	750.7	5.4	0.04
$\phi_{\text{Habitat+Region Ptime+Sex+Age}}$	11	750.8	5.5	0.03
$\phi_{\text{Habitat+TotDens Ptime+Sex+Age}}$	12	752.9	7.5	0.01
$\phi_{\text{Habitat*Region Ptime+Sex+Age}}$	12	752.9	7.5	0.01
$\phi_{\text{Territorial Density Ptime+Sex+Age}}$	8	753.0	7.6	0.01
$\phi_{\text{Rainfall Ptime+Sex+Age}}$	8	754.6	9.2	0.01
$\phi_{\text{Null Ptime+Sex+Age}}$	7	754.6	9.2	0.01
$\phi_{\text{Sex Ptime+Sex+Age}}$	8	756.6	11.3	0.00
$\phi_{\text{Age Ptime+Sex+Age}}$	8	756.7	11.3	0.00
$\phi_{\text{Time Ptime+Sex+Age}}$	10	758.9	13.2	0.00
^a Year sex, and age identified as top covariates for recapture probability through model-selection process.				
^b Key: K, number of estimable parameters; Δ_i , AIC _c deviance; w _i , AIC _s weights.				

Table 4.3 Effects of top predictors (density, habitat, and region) on estimates of annual apparent survival (ϕ).

Region/Habitat/Density	$\phi \pm 1$ SE (95% CI)
Inland	0.56 ± 0.06 (0.45-0.65)
Coastal	0.40 ± 0.04 (0.33-0.47)
Scrub	0.39 ± 0.05 (0.28-0.48)
Mangrove	0.41 ± 0.04 (0.33-0.48)
Wet	0.51 ± 0.07 (0.42-0.61)
Citrus	0.47 ± 0.05 (0.33-0.6)
Low	0.48 ± 0.05 (0.39-0.58)
Mid	0.44 ± 0.03 (0.39-0.5)
High	0.40 ± 0.05 (0.3-0.51)

FIGURES

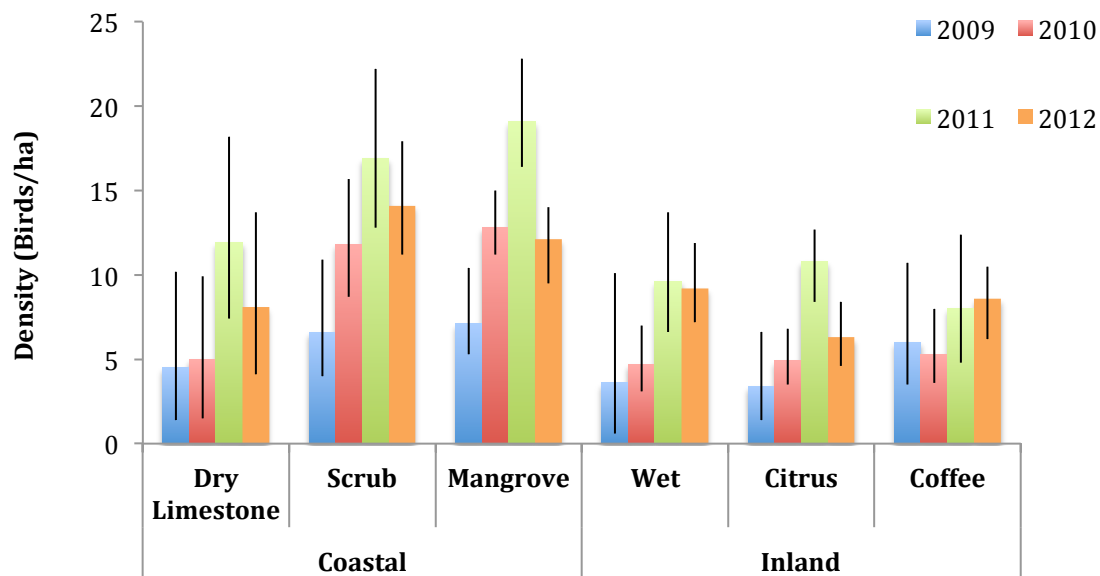


Figure 4.1 Annual mean population density within each habitat and region (coastal, inland) from 2009-2012. Density includes total (territorial plus transient) individuals. (Error bars: 95% confidence intervals)

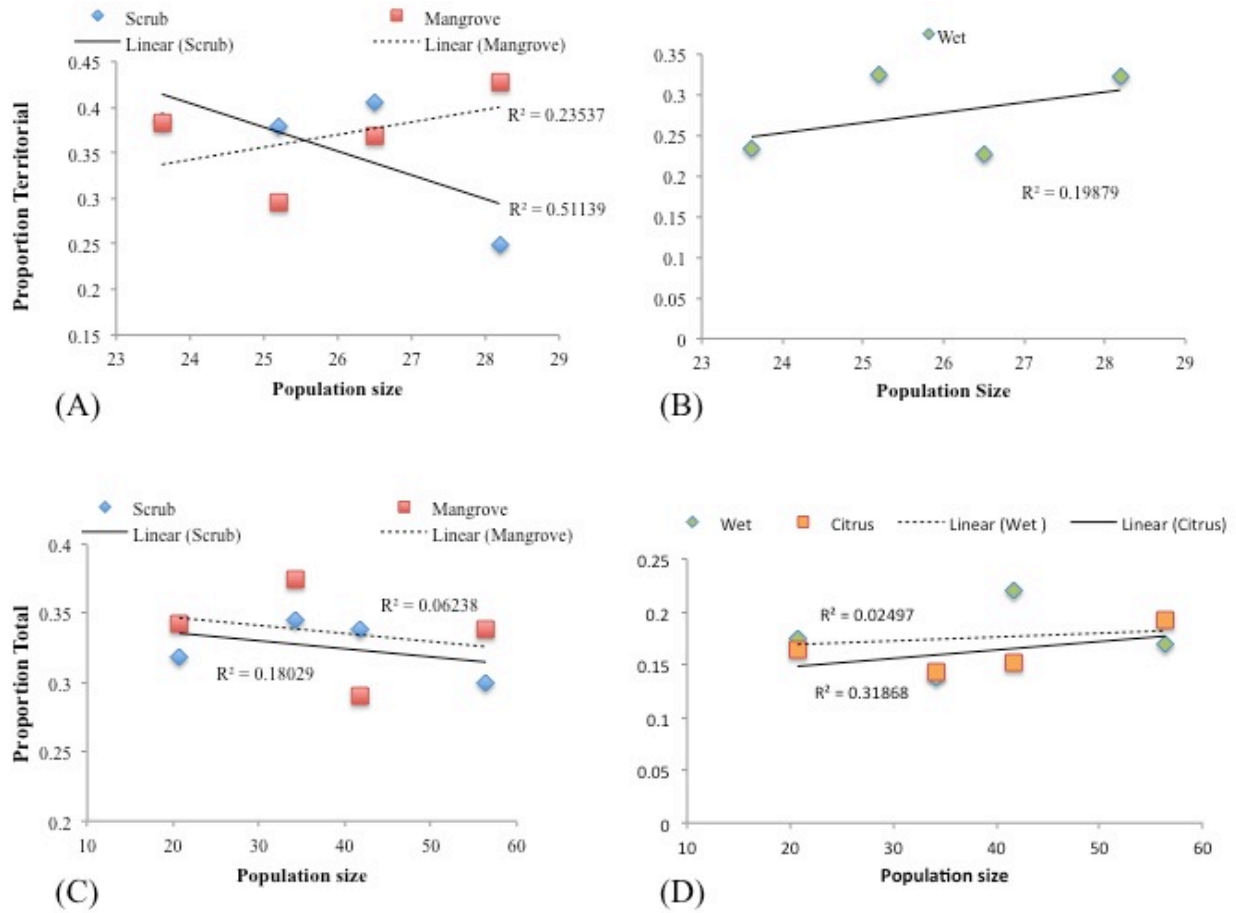


Figure 4.2 (A-D). Relationship between proportional occupancy of each habitat and overall population size for territorial individuals (A, B) and ‘total’ (territorial+transient) individuals (C, D).

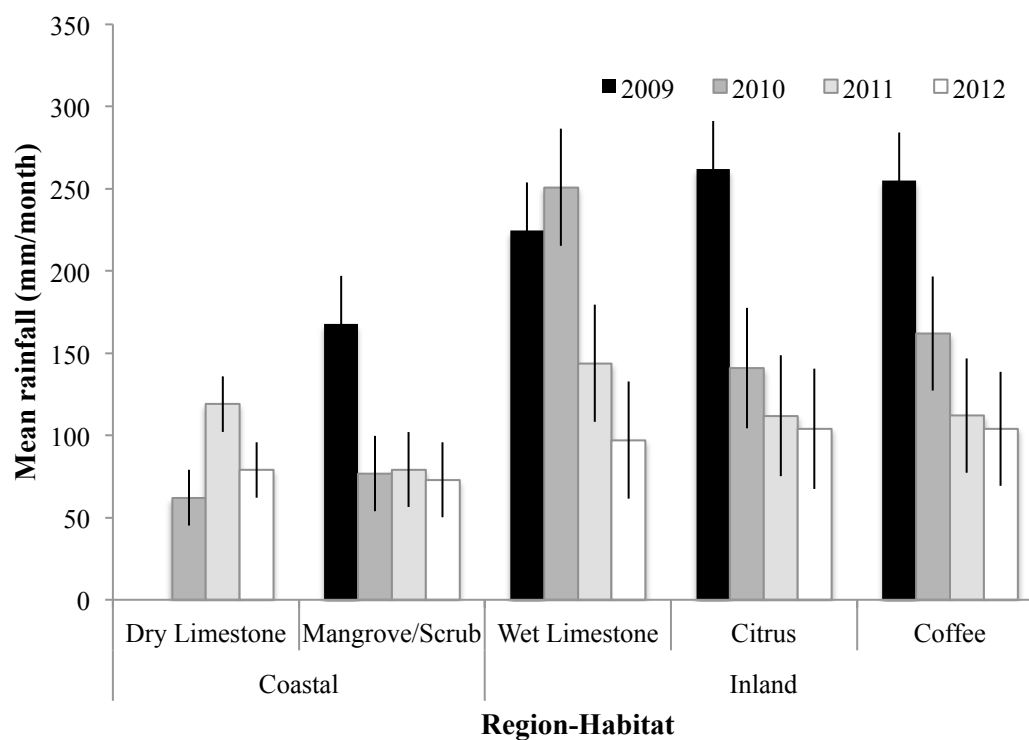


Figure 4.3 Early winter mean rainfall (October-December) from 2009-2012 in each habitat. Error bars: ± 1 SE.

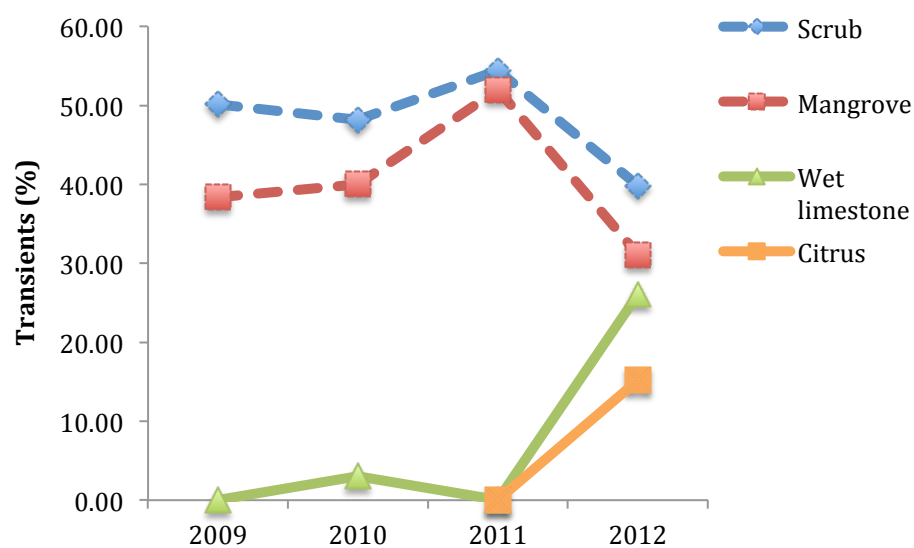
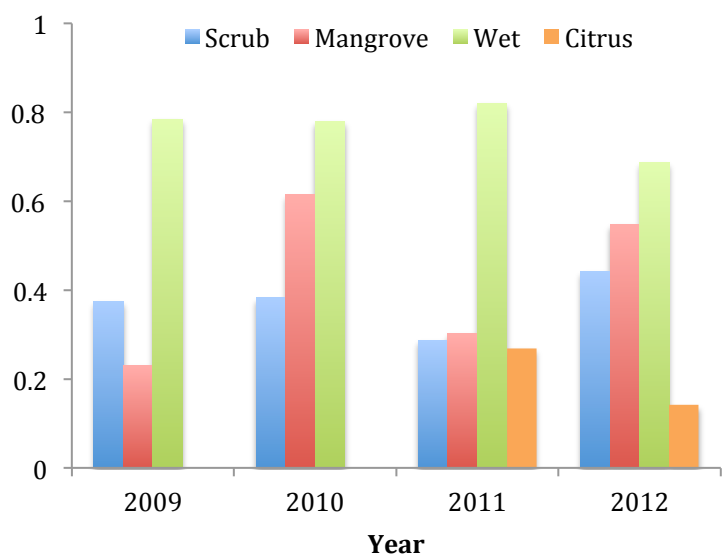


Figure 4.4 Change in proportions of transients captured in coastal (scrub and mangrove) and inland (wet limestone and citrus) habitats annually.



Figures 4.5 Proportion of population departed from each wintering habitat on spring migration, prior to first week of May (May 6th).

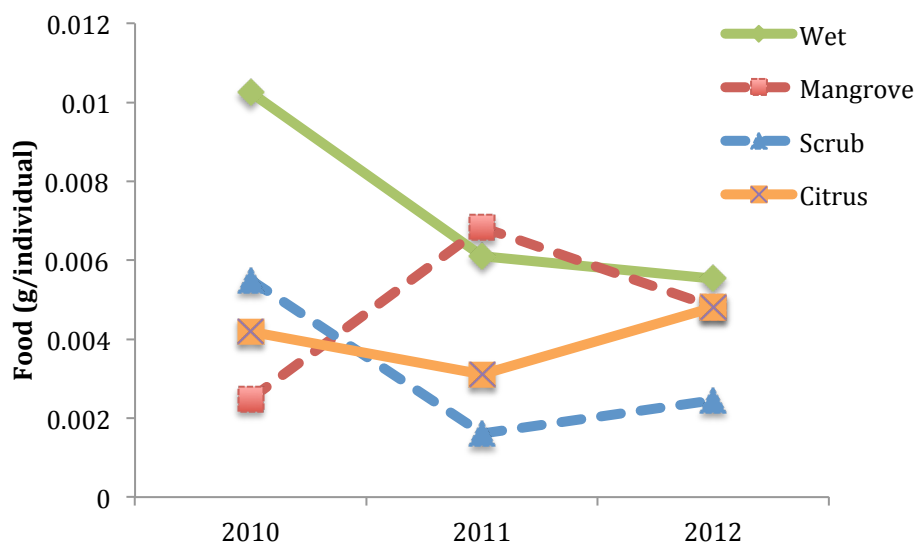


Figure 4.6 Food availability, calculated from annual density within each habitat from 2010-2012.

DISCUSSION

During the four years of this study population abundance of redstarts varied over time and space across six habitats known to differ in suitability for this species (Chapter 3). Besides local and regional changes in density, we documented variation in proportions of transient individuals, annual apparent survival, and departure timing to test for between habitat regulation (buffer effect) and the effects of within-habitat changes in density (crowding effect).

Overall, we found mixed support for a non-breeding buffer effect in redstarts. Our first prediction, that population abundance shifts in high-density years toward proportionately greater use of relatively poor habitats both locally and regionally, was not supported at any spatial scale. Proportions of individuals occupying low suitability habitats did not increase with overall population size. Densities increased uniformly among all habitats as overall population abundance increased, inconsistent with previous findings of buffer effects in winter (Gill et al. 2001). Differences in the variance of within-habitat density also did not correspond with our second prediction from the buffer effect. Instead, variances (CV) were highest in low density, inland wet limestone and citrus habitats compared to coastal scrub and mangrove.

We found support for our second prediction that transience would be density-dependent. Suggestive of a regional buffer effect (see below), very few transients occurred in the high quality inland region and proportions were consistently high in coastal habitats, and increased with population size. This suggests that bird densities were high enough to exclude individuals from territories in both coastal habitats (Kokko and Sutherland 1998, Winker 1998). However, higher proportions of transients occurred

annually in dry scrub, the lowest suitability habitat, which indicated a possible local buffer effect between it and neighboring mangrove. In this lower quality coastal scrub habitat, low food availability may have excluded more individuals from territories, necessitating a transient strategy during the dry season. Concurrently with increased density overall, both territorial and transient numbers increased in mangrove habitat, suggesting that higher food availability there may have compensated for crowding effects to support more individuals.

Interestingly, territorial density in scrub declined as overall population size (Figure 2A) and proportion of transients increased. This is consistent with previous findings that survival of territorial scrub birds was not affected by increasing density (Marra et al. in review). As food declined and population size rose, scrub individuals may have increasingly abandoned a territorial strategy in favor of moving or wandering (Cooper 2015), decreasing competitive interactions with neighbors for food, and allowing the remaining territorial individuals to survive well. At varying spatial scales, both buffer and crowding effects appear to have increased the proportion of transients in low suitability habitats, particularly scrub.

Our third prediction that survival and departure dates of individuals are density-dependent was partially supported. Annual apparent survival was highest in low-density inland habitats (Chapter 3), but annual survival of territorial and transient individuals within any given habitat did not change significantly with increasing population size. This suggests that survival in the highest quality inland habitats may be unaffected by annual fluctuations in density or environmental conditions of the magnitude documented in this study, and thus not regulated by a buffer effect. Spring departure timing varied as

much locally as regionally. Departure timing was consistently earliest in wet limestone and mangrove habitats, latest in scrub and citrus. Sex explained much of the variation in departure timing (males consistently depart earlier than females), with later scrub and citrus departure dates corresponding to proportionally more females in these habitats (Chapter 3). However, in both coastal habitats departure times declined from 2010-2011, consistent with the spike in density. This suggests negative density-dependent feedback of increasing abundances driving greater limitation of individuals at a local scale. One deduction is that different regulatory mechanisms appear to have determined survival and departure timing of redstart populations in the non-breeding season during the years studied here.

Finally, we found partial support for our fourth prediction that food availability would decline in low suitability habitats as overall population size increased. Food availability did decrease with increasing population density, and this occurred in all habitats except mangrove in 2011. This result is unsurprising given that density increased uniformly among all habitats. However, food availability was lowest in poor quality scrub habitat in years of high density, corresponding with later departure dates and greater proportions of transients. As competition for resources likely increased, it appears that a crowding effect (or some form of interference competition; see Poulin et al 1992, Wunderle 1995, Nevoux et al. 2011) pushed individuals into a transient strategy (Sutherland 1996) and delayed their departure for spring migration (Sillett et al. 2004, Marra et al. in review). This provides additional support that crowding effects regulated within-habitat effects of annual density changes, and that transience is affected by both local and regional mechanisms.

Evidence of local and regional density-dependence

Our demographic, but not distributional results are consistent with both local and regional density-dependent mechanisms based on parallels in demographic responses, which supports buffer effects at multiple geographical scales in winter for the first time to our knowledge. Locally, higher quality of mangrove than scrub habitats (Chapter 2, Parrish and Sherry 1994, Johnson and Sherry 2001, Johnson et al. 2006) typically results in higher survival in the former (Marra and Holmes 2001), more males (Marra 2000), earlier departure for spring migration (Studds and Marra 2007, this study), better body condition (Sherry and Holmes 1996, Marra et al. in review) and fewer transients (this study). As population size increased, we documented greater density-dependent feedback on departure dates and proportions of transients in scrub. Brown (1969) predicted that transients (or floaters) occur when increasing population sizes fill up available habitats and force individuals into a non-territorial strategy. Ours is the first study to provide evidence of density-dependent occurrences of transients in non-breeding populations. However, we acknowledge that density did not increase disproportionately in the poorer scrub habitat compared to mangrove, which is inconsistent with a local (coastal) buffer effect at least as it is thought to work (Gill et al. 2001, Ntiamoa-Baidu et al. 2014). Instead, within-habitat crowding effects, particularly considering the number of transient individuals, appear to have negatively impacted individuals more in low quality scrub than mangrove.

In parallel with these local differences in demographic variables, in comparing inland (higher quality—including higher rainfall and correspondingly more food) with coastal habitats, we found evidence for what we argue may be a regional buffer effect.

Inland habitats relative to coastal had the highest annual survival and fewest transients. Additionally, wet limestone forest had the greatest food availability and earliest redstart departure times of any habitat considered. Besides the more favorable demographic rates in the inland habitats, lower average densities (implying reduced intraspecific competition) are consistent with the pattern of a regional buffer effect, suggesting similar density-dependent mechanisms regionally as operated locally between mangrove and scrub habitats. However, we do not know what the carrying capacities are of habitats such as wet limestone (where there may be more intra- or interspecific competition) compared to the higher densities coastally, making it difficult to interpret the density data. Previous work has suggested that the carrying capacity of wet limestone forest may be lower than other habitats for migrants generally, given the low availability of small, hard-bodied arthropods that typify migrant winter diets, as well as the high numbers of interspecific competitors (Johnson et al. 2005).

We also note that a potential explanation for the lack of a spatial buffer effect among all habitats (as opposed to regionally) is the limited spatial and temporal scope of this study. Previous efforts that successfully identified buffer effects used long-term datasets encompassing many more years and sites (Gill et al. 2001, Gunnarsson et al. 2005, Sullivan et al. 2015). These datasets had greater statistical power coupled with larger overall population fluctuations in space and time than we were able to achieve; thus long-term data may be necessary to observe the spatial pattern of buffer effects across larger spatial scales and changes in population size over the course of our study may not have been sufficient to detect large-scale buffer effects.

Additionally, the highest redstart density in year 2011, corresponded with an influx of young (first year) redstarts into Jamaican, evidence of a cohort effect associated with successful reproduction (Sherry et al. 2015). These first-year individuals were naïve with respect to winter habitats, making it possible that environmental conditions in the fall (prior to the first-experienced dry season) made it difficult to assess winter habitat quality. As a result, these individuals may have distributed themselves evenly throughout non-breeding habitats, resulting in no obvious buffer effect of increased population densities.

Effects of multiple regulatory mechanisms on population demography

Transience – The distributions and abundances of transient individuals in this study raise two questions that we address sequentially: First, what determines their abundances, and second, how do these patterns help us understand regulatory mechanisms? For the first question, we suggest a hypothesis to explain the abundances of transients, both among local habitats and regionally. We propose that individual birds generally abandon territories (or are excluded during the settlement period) to become transients when resources are low relative to densities of intraspecific competitors during the non-breeding season. Previous evidence supports the assertion that low resource availability at some time in the winter season can lead to territory abandonment (Lefebvre and Poulin 1992, Lefebvre et al. 1994, Cooper et al. 2015). In our study, more transients in the high density, low food coastal habitats supported a regional buffer effect on transience. Higher abundances of transients in our coastal than inland region is particularly relevant to regulatory mechanisms, because the transient individuals were

captured within the habitats (Chapter 2), and would potentially have been able to exert more crowding effects via their food consumption than would be the case with territorial individuals. Within the coastal region, we also found that scrub had consistently higher proportions of transients than mangrove, which provides evidence of territorial exclusion or abandonment in poorer habitats via crowding effects. While we cannot verify that all of the transient individuals we observed were truly non-territorial, because multi-territoriality or large home ranges are a possibility, the fact that we found more transients both locally and regionally where resources appear to be less available suggests that many of these individuals were in fact transients (Winker et al. 1995, Latta and Faaborg 2001, 2002, Brown and Long 2007). Transient individuals were also more likely than territorial to be socially subordinate – yearling males and females – suggesting they were likely not territorial elsewhere. These results involving transient individuals are the first to suggest that winter spatial behavior can provide insight into the effects of regulatory mechanisms on wintering populations of migratory birds.

Spring departure timing—Departure timing provides additional evidence of the benefits of resource buffering in high quality wet limestone habitat. Cooper et al. (2015) show experimentally that food reduction delays spring migration. However, departure dates of wet limestone individuals were not affected by increasing densities and reductions in food availability. While sex plays a role in determining departure time, both mangrove and wet limestone habitats were male-dominated yet the latter had consistently earlier departure dates, so individuals' sex cannot be the only explanation. Individuals occupying high quality wet limestone forest appear to have been buffered against the kind of negative density-dependent feedback (crowding effect; Rodenhouse et

al. 1997) that is important, or at least stronger in mangroves (Cooper et al. 2015, Marra et al. in review); and abundance of transients in coastal habitats may have contributed as argued in the previous section.

Carryover effects resulting from delayed spring departure are likely to limit reproductive success of individuals occupying habitats of lower suitability in winter (Gordo et al. 2005, 2007, Duriez et al. 2012, Finch et al. 2014). While we were unable to include estimates of physiological condition as part of this study, past research on American redstarts and other migratory species have demonstrated that carryover effects are linked to poorer condition of individuals in late winter (Studds and Marra 2005, Cooper et al. 2015); and poorer body condition also predicts poor annual survival (Johnson et al. 2006). Thus carryover effects are critical for understanding how regulatory mechanisms in winter affect population dynamics of migratory species year-round (Runge and Marra 2005, Gordo et al. 2007, Rockwell et al. 2012, Finch et al. 2014).

Survival—Higher survival rates in wet limestone forest than mangrove habitats was a surprising result, given past research on redstart populations in Jamaica (Marra and Holmes 2001, Johnson et al. 2006). Comparisons with estimates from previous years show that our more recent wet limestone survival rates were similar to past estimates of mangrove male survival in years when average density was much lower (5-8 birds/ha; Marra et al. in review). This suggests that survival has declined with increasing density over a lengthy period of time in coastal habitats. Locally, greater resource competition from high densities of territorial conspecifics and resident competitors (e.g., Yellow Warbler ()), increasing numbers of transients, and increasing drought conditions since the

mid-1990s (Studds and Marra 2007, Marra et al. in review) may have contributed to these declines, consistent with a buffer effect on annual survival.

Implications for population persistence and regulation

Our findings are the first to demonstrate density-dependent demographic responses of non-breeding redstart populations consistent with both crowding and buffer effects. Redstarts occupying low quality coastal habitats, particularly dry scrub, appear to be more vulnerable to crowding effects from increasing density and overwinter resource limitation (Johnson et al. 2001, Marra and Holmes 2001, Studds and Marra 2005). Both buffer and crowding effects increased the prevalence of transient behaviors and the strength of winter carryover effects (Studds and Marra 2005, Cooper et al. 2015). These effects suggest that individuals occupying such seasonally unstable (Parrish and Sherry 1994) habitats are likely to be most susceptible to anthropogenic disturbances and shifting climatic conditions (Silleet et al. 2000, Newton 2004, Nevoux 2008, Ockendon et al. 2014a).

Increasing transience with overall population size may be interpreted as another type of buffering than what has been studied to date in the literature on non-breeding bird populations, reducing competition amongst territorial birds, while allowing transients to pursue resources independently (Brown and Long 2007, Brown and Sherry 2008). The present study has shown that strong territoriality in habitats like mangrove did not exclude all transients; consistent with previous studies that winter transients will push into higher quality sites to access greater food resources (Brown and Long 2007, Brown and Sherry 2008, Smith et al. 2011). In high-density years, increasing numbers of individuals may opt for a transient strategy, avoiding agonistic territorial interactions but

benefiting from proximity to mangrove resources. In this case, alternative behaviors may actually decrease the overall vulnerability of redstarts to annual changes in winter conditions (Petit et al. 1995). More work is needed to clarify the conditions (e.g., body condition, survival, departure times) and possible effects of transient individuals on population processes, but our study sheds light on the range and impact of alternative spatial behaviors in territorial, non-breeding populations.

Overall, our study supports the assertion that density interacts with habitat quality to regulate redstart populations in the non-breeding season, but it is important to note that habitat and/or region remain the best overall predictors of demographic rates. Relatively high resource availability in wet limestone forest, stemming from lower densities and higher rainfall, make this a critical habitat for buffering winter redstart populations against both population fluctuations and resource limitation. Large tracts of wet forest remain in Jamaica's interior, but these are highly threatened by agricultural conversion, housing development, and timber harvesting, as are most wet forests throughout the Caribbean (Chai et al. 2009, Newman et al. 2014). Conservation strategies should be careful not to focus only on densely occupied regions, but to also consider the value of maintaining more predictable, buffered habitats.

Chapter 5

Synthesis and Conclusions: Are Redstart populations regulated by within and between habitat mechanisms in the non-breeding season?

Populations can be regulated at a local or regional scale when habitat suitability varies and greater abundances reduce fitness as proportionately more individuals are pushed into poorer habitats (Newton 1998, Rodenhouse et al. 2003). When population abundance is high, this results in a buffer effect, where greater increase of local densities in poor quality habitats leads to greater variance in population size from year to year (Kluyver and Tinbergen 1953, Brown 1969). In territorial species, behavioral dominance mechanisms drive these patterns by limiting occupancy of more suitable habitats via competitive interactions for food and/or space, i.e. crowding effects (Pulliam and Danielson 1991, Newton 1998). Subordinate individuals must either occupy territories in poorer habitats where competition for resources is less intense (Brown 1969, Fretwell 1972, Rodenhouse et al. 1997) or adopt an alternative spatial behavior like transience (Kokko and Sutherland 1998). The only studies that have tested mechanisms of population regulation in non-breeding birds to date assessed either within or between habitat effects (Gill et al. 2001, Ntiamoa-Baidu 2014, Marra et al. in review), but not how these may simultaneously affect population distribution and demography. The present study tested both the buffer and crowding effect hypothesis in non-breeding populations

of a long-distance migratory songbird, the American redstart. Redstarts occupy diverse habitats in winter (Sliwa and Sherry 1992) and are highly territorial (Marra et al. 1993, Marra 2000), two necessary conditions for a buffer effect. Testing this necessitates accurate estimates of population densities in different habitats, a gradient in habitat suitability, and evidence for effects of density on habitat suitability and demography within and/or among habitats, the topics of chapters 2-4, respectively.

Accurate estimation of population density is challenging in the non-breeding season because (1) individuals may be less conspicuous; and (2) variation in individual space-use behaviors (e.g. territoriality, multi-territoriality, and transience) may increase heterogeneity of their detectability and movement. Many migratory passerines have both territorial and non-territorial individuals in winter populations (Rappole et al. 1989, Winker et al. 1990, Lefebvre et al. 1994, Wunderle 1995, Latta and Faaborg 2001, 2002, Smith et al. 2010, Brown and Sherry 2008, Kresnik and Stutchbury 2014). The occurrence of transients in territorial populations is not surprising: The very benefit of territoriality is that some individuals are excluded, which necessitates alternatives like transience.

In the present study, estimates of redstart density using distance-sampling methods were substantially greater than territorial density estimates (Chapter 2). In this chapter, I argued that the former method likely detects individuals that are transient in a given habitat, but present at the time of surveys. To assess this possibility quantitatively, I compared mist-net captured individuals with territorial individuals, which represents the first proposed method for quantifying abundance of transients and identifying them as individuals. My findings from this comparison supported the conclusion that some

wintering habitats contained a substantial number of non-territorial individuals. While these data cannot account for when and how long transient individuals remained in these habitats, their consistent presence and proportions over time suggests they may be relevant to population processes (Brown and Long 2007, Lenda et al. 2012).

We know little about what transient individuals actually do in most species, but possibilities include temporary transience (e.g., in response to particular weather events or changes), season-long transience, multiple territoriality, overlapping territorial individuals, or a combination of these strategies (Rappole 1989, Winker 1998, Brown and Long 2007). One weakness of my results is that individuals identified as transients in one habitat could theoretically be undetected territory holders from an area outside our research sites. Although this is possible, and more work is needed to track individual redstarts throughout the non-breeding season, an important argument against this idea is that transients in the present study tended to be comprised of relatively subordinate classes of individuals, especially females and yearling males (Chapter 2). Subordinate individuals are the most likely to abandon or be excluded from a territorial strategy when winter conditions no longer favor it.

The buffer effect depends on variation in the suitability of habitats in the non-breeding season typically corresponding with food availability (for examples of food-related habitat heterogeneity see Lefebvre and Poulin 1996, Strong and Sherry 2000, Brown and Sherry 2006, Danner et al. 2013). Food availability has often been linked to rainfall and moisture levels (Silleet et al. 2000, Smith et al. 2010, Wilson et al. 2011, Ockendon et al. 2014a). In the non-breeding season, survival, winter carryover effects, and spatial behavior are typically limited by habitat suitability, especially food (Wunderle

1995, Latta and Faaborg 2001, 2002, Johnson et al. 2006, Townsend et al. 2011, 2012).

In Jamaica, I found that habitats indeed differ in relative suitability for redstarts (Chapter 3), and that these differences affected individuals at both local (neighboring) and regional spatial scales (Chapter 3). Redstarts overwintering in inland, montane habitats (wet limestone forest and citrus) had higher annual apparent survival and were less likely to be transients than birds occupying coastal scrub and mangrove. These differences correspond to greater rainfall in the inland region of western Jamaica, as well as greater food availability in wet limestone forest. Both mangrove and wet limestone redstart populations had higher ratios of socially dominant individuals (adult males) and earlier spring departures than their neighboring habitats within the same regions. Thus population indicators support variation in habitat suitability, but some are weighted by local and others regional differences in ecological conditions.

Including multiple regions within a large non-breeding area like Jamaica revealed a more complex gradient of habitat suitability than previously documented for this species (Johnson et al. 2006). Expanding detailed demographic studies into interior habitats showed that density corresponded with regional differences in habitat suitability, but not local (Chapter 3). High survival and few transients in both inland habitats, despite differences in redstart age/sex structure and even food availability, suggests ecological buffering against changing population size as well as climatic conditions. Additionally, relatively high proportions of transient individuals in coastal habitats corresponded with higher densities there, suggesting these individuals may be important indicators of both habitat suitability (more transients in less suitable habitats) and the

effects of population regulation on spatial behavior, i.e. reduced territoriality when conditions are poor (Fretwell 1972, Kokko and Sutherland 1998, Brown and Long 2007).

Patterns of change in density and how these affect population characteristics both within and among habitats determine whether population regulation is occurring. Previous work on non-breeding migratory birds demonstrated a buffer effect on distribution and survival over large spatial scales (Gill et al. 2001, Gunnarsson et al. 2005, Ntiamoa-Baidu et al. 2014), but these studies found that poorer habitats characterized by less food experienced the greatest increase in density and subsequently negative feedback on average (multiple-habitat) population vital rates like survival. In comparison, I found that a buffer effect does not cause greater increases or variance of density in low suitability habitats (Chapter 4). Instead, densities are consistently lower within high quality inland regions and high in low quality coastal habitats. In the high quality inland region, higher survival, fewer transients, and earlier departure times (in wet limestone only) relative to coastal habitats provided evidence to support a buffer effect on redstart demography. Within habitats, increasing overall population size and within-habitat densities decreased resource availability more in relatively low suitability habitats. Lower food availability per individual appeared to delay spring departure and increase proportions of transient individuals, particularly in coastal scrub habitat, suggesting a crowding effect of increased competition (Sillett et al. 2004, Grunkorn et al. 2014, Marra et al. in review). Population regulation is supported, but the underlying mechanisms vary both regionally and by habitat, rather than a single consistent mechanism regulating populations across a winter landscape (e.g. Gill et al. 2001).

One of the strongest kinds of evidence I discovered for population regulation in redstarts is the variation in proportions of transients both among and within non-breeding habitats over time. Greater numbers of transients in coastal habitats corresponded to a regional buffer effect, while increased proportions of transients within mangrove and scrub indicated both a local buffer and crowding effects on territorial behavior (Chapter 4). Furthermore, transient individuals tend to be socially subordinate (Chapter 2), likely relegated to this strategy by increased competition for declining resources. While transient individuals (or floaters, non-territorial individuals) have been documented in many species of migratory songbirds—e.g., Wood Thrushes (Rappole et al. 1989), Black-throated blue Warblers (Wunderle 1995), Prairie Warblers (Latta and Faaborg 2001), Cape May Warblers (Latta and Faaborg 2002), Northern Waterthrush (Smith et al. 2010)—we know little about the specifics of transient behaviors and what effects, if any, they may have on overwintering population dynamics (Brown and Long 2007). Removal experiments in winter have shown that unknown individuals often move into vacated territories (Morton et al. 1987, Marra et al. 1993, Stutchbury 1994), suggesting that transients may be able to mask buffer the effects of population declines (Durrell et al. 2004).

One possible explanation for the large numbers of transients documented in the present study is that conditions may have been unusual in 2009-2012 due to category 5 Hurricane Ivan (the 6th most intense Atlantic hurricane on record; Stewart 2005), which passed just south of Jamaica on September 11-12, 2004. This storm did the most severe damage to mangrove trees and other south coast Jamaican vegetation in our Font Hill study sites since research began there in 1986, which may have affected the quality and

quantity of habitat dramatically. To assess this possibility I used methods developed in Chapter 2 to quantify the number of transient individuals captured on mangrove and scrub sites going back to 1995. I used only the years for which mark-recapture-resighting efforts were consistent with more current field efforts. Results (Fig. 5.1) indicate consistently high proportions of transients (40-50% of marked and captured birds, and in rare cases up to 70%) going back to the mid-1990s, consistent with more recent estimates in the years of this study (2009-2012).

These long-term data showed that proportions of all individuals that were transients have been consistently greater in lower suitability scrub habitat compared to mangroves. This supported the hypothesis that transience results in part from competition with dominant individuals over limited resources (Kokko and Sutherland 1998, Lopez-Sepulcre and Kokko 2005, Brown and Long 2007). Long-term occurrence of transients in our study areas suggested not only that these individuals are a normal part of the non-breeding population in some habitats, but also that regulatory mechanisms incorporating transience may be applicable to other species of long-distance migratory birds (see the list of species with documented transience above).

Additionally, a conspicuous increase in the number of transient individual redstarts occurred in the January-April 2005 and 2006 seasons, and in both habitats (Fig. 5.1). Although I do not know definitively what caused this apparent increase, I suggest hurricanes as the most likely cause. Hurricane Ivan (see above) struck our study areas and did considerable damage throughout Jamaica beginning prior to the 2005 winter field season. One possible mechanism is that hurricanes may cause sufficient damage to vegetation in large areas of south coastal Jamaica within and around our study areas as to

reduce food availability, and thus force proportionately more individuals into transience. Besides hurricanes, unusually cold and rainy conditions in wintering habitats appear to cause individuals to become transients (Rappole et al. 1989, Winker et al. 1990), and in the present study drought conditions during the subtropical dry season resulted in low food availability in late winter and intensified density-dependent competition in some habitats more than others (Chapter 4, Parrish and Sherry 1994). What all three ecological circumstances share is seasonally or abruptly deteriorating habitat quality during the non-breeding season when long-distance migrants are present in the tropics.

In conclusion, findings presented in this study support the hypothesis that a regional buffer effect regulates survival, departure, and transience of redstarts between inland and coastal regions. Ecologically driven food limitation combines with higher densities to regulate populations overwintering in relatively low quality habitats via increased competition (a crowding effect). Additionally, we established that transients are useful indicators of both habitat quality and mechanisms of population regulation in a wintering migratory songbird. Although this dissertation has raised as many questions as it has addressed, it identifies directions of important non-breeding season considerations necessary to understand population limitation and regulation in migratory animals. These considerations are critical not only for addressing regulatory mechanisms in multiple-habitat and wide-ranging animals like migratory birds, but also for helping predict how these animals will respond to rapidly changing environments caused by diverse global change phenomena including climate change and habitat loss.

FIGURES

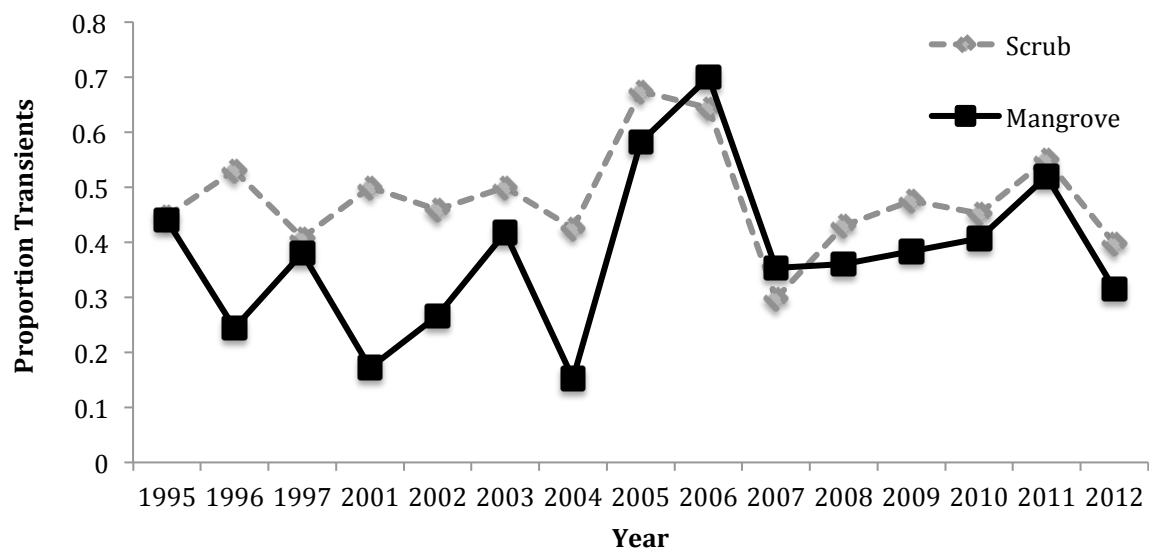


Figure 5.1 Proportion of birds captured annually that were transient, i.e. did not defend a territory in either the site they were captured or neighboring sites. Data shown from 1995-1997, 2001-2012.

LITERATURE CITED

- Arendt, W. J. (1992). Status of North American migrant land- birds in the Caribbean: a summary. Pages 143–171 in J. Hagan and D. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.
- Ashbrook, K., Wanless, S., Harris, M.P., & Hamer, K.C. (2010). Impacts of poor food availability on positive density dependence in a highly colonial seabird. *Proceedings of the Royal Society, Biological Sciences* 277:2355-2360.
- Balbontin, J., & Ferrer, M. (2008). Density-dependence by habitat heterogeneity: individual quality versus territory quality. *Oikos* 117:1111–1114.
- Becker, B.H., Press, D.T., & S.G. Allen. (2009). Modeling the effects of El Nino, density-dependence, and disturbance on harbor seal (*Phoca vitulina*) counts in Drakes Estero, California: 1997-2007. *Marine Mammal Science* 25(1):1-18.
- Begon, M., Harper, J.L., & Townsend, C.R. (1996). Ecology. Individuals, populations and communities. Blackwell Scientific Publications, Oxford.
- Betini, G. S., Griswold, C. K., Prodan, L., & Norris, D. R. (2014). Body size, carry-over effects and survival in a seasonal environment: consequences for population dynamics. *Journal of Animal Ecology* 83:1313–1321.
- Betini, G. S., Griswold, C. K., & Norris, D. R. (2013). Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. *Proceedings of the Royal Society B* 280: 20130110.
- Betts, M. G., Hadley, A. S., Rodenhouse, N., & Nocera, J. J. (2008). Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings. Biological Sciences / The Royal Society* 275(1648): 2257–63.
- Borgmann, K.L.C., Pearson, S.F., Levey, D.J., & Greenberg, R. (2004). Wintering yellow-rumped warblers (*Dendroica coronate*) track manipulated abundance of myrica cerifera fruits. *The Auk* 121(1): 74-87.
- Both, C., Sanz, J., Artemyev, A., Blaauw, B., Cowie, R., Dekhuizen, A., & Zang, H. (2006). Pied Flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe : differential effects of winter and migration conditions on breeding date. *Ardea* 94(3): 511–525.
- Both, C., Van Turnhout, C. A.M., Bijlsma, R. G., Siepel, H., Van Strien, A. J., & Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings. Biological Sciences / The Royal Society* 277(1685): 1259–66.

- Bradshaw, C.J.A., Davis, L.S., Lalas, C. & Harcourt, R.G. (2000). Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. *Journal of Zoology* 252: 41-51.
- Brouwer, L., Tinbergen, J.M., Both, C., Bristol, R., Richardson, D.S. and J. Komdeur. (2009). Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine. *Ecology* 90(3): 729-741.
- Brown, D. R. & Long, J. A. (2007). What Is a Winter Floater? Causes, consequences, and implications for habitat selection. *The Condor* 109(3): 548-565.
- Brown, D. R., & Sherry, T. W. (2008). Alternative strategies of space use and response to resource change in a wintering migrant songbird. *Behavioral Ecology* 19(6): 1314-1325.
- Brown, J. L. (1969). The buffer effect and productivity in tit populations. *American Naturalist* 103(932): 347-354.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) Introduction to Distance Sampling. Oxford University Press, New York.
- Burnham, K. P., & Anderson, D.R. (2002). Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer Science and Business Media, Fort Collins, Colorado, USA.
- Calvert, A. M., Walde, S. J., & Taylor, P. D. (2009). Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. *Avian Conservation and Ecology* 4(2): 5. [online] URL: <http://www.ace-eco.org/vol4/iss2/art5>
- Caplins, S. A., Gilbert, K. J., Ciotir, C., Roland, J., Matter, S. F., & Keyghobadi, N. (2014). Landscape structure and the genetic effects of a population collapse. *Proceedings. Biological Sciences / The Royal Society* 281: 20141798.
- Catry, P., A. Campos, V. Almada, & Cresswell, W. (2004). Winter segregation of migrant European Robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology* 35: 204-209.
- Chai, S., Tanner, E., & McLaren, K. (2009). High rates of forest clearance and fragmentation pre- and post-national park establishment: the case of a Jamaican montane rainforest. *Biological Conservation* 142(11): 2484-2492.
- Chalfoun, A. D., & Martin, T. E. (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, 44(5): 983-992.
- Chalfoun, A. D., F. R. Thompson, & Ratnaswamy, M.J. (2002). Nest predators and fragmentation: a review and meta- analysis. *Conservation Biology* 16: 306-318.
- Chandler, R. (2011). Distance sampling analysis in unmarked. R Foundation for Statistical Computing 1-8.
- Chandler, R. B. & King, D. I. (2011). Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. *Journal of Applied Ecology* 48(4): 1038-1047.

- Cimprich, D. (2009). Effect of Count Duration on Abundance Estimates of Black-Capped Vireos. *Journal of Field Ornithology* 80(1): 94–100.
- Cooper, N. W., Thomas, M. A., Garfinkel, M. B., Schneider, K. L., & Marra, P. P. (2012). Comparing the precision, accuracy, and efficiency of branch clipping and sweep netting for sampling arthropods in two Jamaican forest types. *Journal of Field Ornithology*, 83(4): 381–390.
- Cooper, N., T. W. Sherry, and P. P. Marra. (2015). Experimental reduction of winter food availability decreases body condition and delays spring migration in a long-distance migratory bird. *Ecology*, available early on-line: <http://www.esajournals.org/doi/abs/10.1890/14-1365.1>.
- Cresswell, W. (2014). Migratory connectivity of Palaearctic – African migratory birds and their responses to environmental change : the serial residency hypothesis. *Ibis* 156(3): 493–510.
- Dail, D. & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67: 577–587.
- Danner, R. M., Greenberg, R. S., Danner, J. E., Kirkpatrick, L. T., & Walters, J. R. (2013). Experimental support for food limitation of a short-distance migratory bird wintering in the temperate zone. *Ecology* 94(12): 2803–2816.
- Davies, N.B. & Houston, A.I. (1981). Owners and satellites: the economics of territory defense in the Pied Wagtail, *Motacilla alba*. *Journal of Animal Ecology* 50:157–180.
- Dhondt, A.A. (2011). Interspecific Competition in Birds. Oxford University Press, London.
- Diggs, N.E., Marra, P.P. & Cooper, R.J. (2011). Resource limitation drives patterns of habitat occupancy during the nonbreeding season for an omnivorous songbird. *The Condor* 113(3): 646–654.
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science* 345(6195): 401–406.
- Duriez, O., Ens, B. J., Choquet, R., Pradel, R., & Klaassen, M. (2012). Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. *Oikos* 121(6): 862–873.
- Durell, S. E. A. Le V. dit., & Clarke, R. T. (2004). The buffer effect of non-breeding birds and the timing of farmland bird declines. *Biological Conservation* 120(3): 375–382.
- Evelyn, O.B. & Camirand, R. (2003). Forest cover and deforestation in Jamaica: an analysis of forest cover estimates over time. *International Forestry Review* 5: 354–363.
- Eyre, L.A. (1979). Quasi-Urban Melange Settlement: Cases from St. Catherine and St. James, Jamaica. *Geographical Review* 69(1): 95–100.
- Eyre, L.A. (1986). Jamaica: Test Case for Tropical Deforestation. *Ambio* 16(6): 338–343.
- Faaborg, J. & Holmes, R., (2010). Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80(1): 3–48.
- Farnsworth, G., Pollock, K., & Nichols, J. (2002). A removal model for estimating detection probabilities from point-count surveys. *The Auk* 119(2): 414–425.

- Farrell, S. L., Morrison, M. L., Campomizzi, A. J., & Wilkins, R. N. (2012). Conspecific cues and breeding habitat selection in an endangered woodland warbler. *The Journal of Animal Ecology* 81(5): 1056–1064.
- Ferrer, M., Belliure, J., Minguez, E., Casado, E., & Bildstein, K. (2014). Heat loss and site-dependent fecundity in chinstrap penguins (*Pygoscelis antarctica*). *Polar Biology* 37: 1031–1039.
- Ferrer, M., & Donazar J.A. (1996). Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology* 77: 69–74.
- Finch, T., Pearce-Higgins, J. W., Leech, D. I., & Evans, K. L. (2014). Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodiversity and Conservation* 23(10): 2427–2444.
- Fretwell, S. D., and H. L. Lucas. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Fretwell, S. D. (1972). Populations in a seasonal environment. Princeton University Press, Princeton, NJ.
- Gale, G. A., Round, P. D., Pierce, A. J., Nimnuan, S., Pattanavibool, A., & Brockelman, W. Y. (2009). A Field Test of Distance Sampling Methods for a Tropical Forest Bird Community. *The Auk* 126(2): 439–448.
- Garton, E. & Kissling, M. (2006). Count Surveys: A Combination of Distance and Double-Observer Sampling. *The Auk* 123(3): 735–752.
- Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W., & Sutherland, W. J. (2001). The buffer effect and large-scale population regulation in migratory birds. *Nature* 412(6845): 436–8.
- Glas, P. (1960). Factors governing density in the Chaffinch (*Fringilla coelebs*) in different types of wood. *Arch. Neerlandaises Zool.* 13:466-472.
- Gómez-Montes, C. & Bayly, N. (2010). Habitat use, abundance, and persistence of Neotropical migrant birds in a habitat matrix in northeast Belize. *Journal of Field Ornithology* 81(3): 237–251.
- Gordo, O., Brotons, L., Ferrer, X., & Comas, P. (2005). Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology* 11(1): 12–21.
- Gordo, O. & Sanz, J. J. (2007). The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *Journal of Ornithology* 149(2): 199–210.
- Grande, J. M., Serrano, D.S., Tavecchia, G., Carrete, M., Ceballos, O., Díaz-Delgado, R., Tella, J.L., & Donazar, J. A. (2009). Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* 118(4): 580–590.
- Greenberg, R. (1995). Insectivorous Migratory Birds in Tropical Ecosystems: The Breeding Currency Hypothesis. *Journal of Avian Biology* 26(3): 260-264.

- Greenberg, R. & Salewski, V. (2005). Ecological Correlates of Wintering Social Systems in New World and Old World Migratory Passerines. In: Greenberg, R., Marra, P.P. (Editors), *Birds of Two Worlds: The Ecology and Evolution of Migration*, Johns Hopkins University Press, Baltimore, pp. 291-30.
- Gross, S. & Price, T. (2000). Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography* 27: 869-878.
- Grünkorn, T., Potiek, A., Looft, V., Jonker, R. M., Chakarov, N., & Krüger, O. (2014). Territory quality affects the relative importance of habitat heterogeneity and interference competition in a long-lived territorial songbird. *Journal of Avian Biology* 45: 15–21.
- Gunnarsson, T. G., Gill, J. A., Petersen, A., Appleton, G. F., & Sutherland, W. J. (2005). A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology* 74(5): 965–971.
- Henaus, V., Bregnballe, T., & Lebreton, J.D. (2007). Dispersal and recruitment during population growth in a colonial bird, the Great Cormorant. *Journal of Avian Biology* 38: 44-57.
- Hines, J., Kendall, W.L., & Nichols, J. (2003) On the use of the robust design with transient capture-recapture models. *The Auk* 120:1151-1158.
- Hixon, M.A., Pacala, S.W., & Sandin, S. A. (2002). Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83(6): 1490–1508.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., & Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509.
- Hollander, F. A., Van Dyck, H., San Martin, G., & Titeux, N. (2011). Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *PloS One*, 6(9): e25703.
- Hollander, F. A., Titeux, N., & Dyck, H. (2012). Territorial resource valuation deviates from habitat quality in an ecologically trapped, long-distance migratory bird. *Behavioral Ecology and Sociobiology* 66(5): 777–783.
- Hollander, F. A., Titeux, N., & Van Dyck, H. (2013). Habitat-dependent prey availability and offspring provisioning explain an ecological trap in a migratory bird. *Functional Ecology* 27(3): 702–709.
- Jirinec, V., Campos, B. R., & Johnson, M. D. (2011). Roosting behaviour of a migratory songbird on Jamaican coffee farms: landscape composition may affect delivery of an ecosystem service. *Bird Conservation International* 21(03): 353–361.
- Johnson, E., DiMiceli, J., Stouffer, P., & Brooks, M. (2011). Habitat use does not reflect habitat quality for Henslow's Sparrows (*Ammodramus henslowii*) wintering in fire-managed longleaf pine savannas. *The Auk* 128(3): 564–576.
- Johnson, M. D. (2007). Measuring habitat quality : a review. *The Condor* 109(3): 489–504.
- Johnson, M., & Sherry, T. (2001). Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70: 546–560.

- Johnson, M. D., Levy, N. J., Kellermann, J. L. & Robinson, D. E. (2009). Effects of shade and bird predation on arthropods and leaf damage on coffee farms in the Blue Mountains. *Agroforestry Systems* 76: 139-148.
- Johnson, M. D., Kellermann, J. L. & Stercho, A. M. (2010). Pest reduction services by birds in shade and sun coffee in Jamaica. *Animal Conservation* 13: 140-147.
- Johnson, M. D., Sherry, T. W., Holmes, R. T., & Marra, P. P. (2006). Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conservation Biology* 20(5): 1433-44.
- Johnson, M.D., Sherry, T.W., Strong, A.M., & Medori, A. (2005). Migrants in Neotropical bird communities: an assessment of the breeding currency hypothesis. *Journal of Animal Ecology* 74: 333-341.
- Katti, M. & Price, T.D. (1996). Effects of climate on Palearctic warblers over-wintering in India. *Journal of the Bombay Natural History Society* 93: 411-427.
- Kennedy, C. & Marra, P. (2010). Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs* 80(4): 651-669.
- Kéry, M., Royle, J., & Schmidt, H. (2005). Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. *Ecological Applications* 15(4): 1450-1461.
- Kluyver, H.N. & Tinbergen, L. (1953) Territory and the regulation of density in titmice. *Archives of Néerl De Zoology* 10: 265-289.
- Kokko, H. & Sutherland, W. (1998). Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *The American Naturalist* 152(3): 354-366.
- Kokko, H., Harris, M., & Wanless, S. (2004). Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology* (73): 367-376.
- Koronkiewicz, T. & Sogge, M. (2006). Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. *The Condor* 108(3): 558-570.
- Kresnik, R. J. & Stutchbury, B. J. M. (2014). Space-use strategies of wintering Ovenbirds in Belize: causes and consequences. *Journal of Field Ornithology* 85(3): 274-288.
- Laake, J.L. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA.
- Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Lack, D. (1976). *Island biology as illustrated by the land birds of Jamaica*. Blackwell Scientific Publications, Oxford, UK.
- Larivière, S., & Messier, F. (1998). Effect of Density and Nearest Neighbours on Simulated Waterfowl Nests: Can Predators Recognize High-Density Nesting Patches? *Oikos* 83(1): 12-20.

- Latta, S. C. (2012). Avian research in the Caribbean: past contributions and current priorities. *Journal of Field Ornithology* 83(2): 107–121.
- Latta, S. & Faaborg, J. (2001). Winter Site Fidelity of Prairie Warblers in the Dominican Republic. *The Condor* 103(3): 455–468.
- Latta, S. & Faaborg, J. (2002). Demographic and Population Responses of Cape May Warblers Wintering In Multiple Habitats. *Ecology* 83(9): 2502–2515.
- Lebreton, J. D., Burnham, K.P., Clobert, J., & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lefebvre, G. & Poulin, B. (1996). Seasonal Abundance of Migrant Birds and Food Resources in Panamanian Mangrove Forests. *The Wilson Bulletin* 108(4): 748–759.
- Lefebvre, G., Poulin, B., & McNeil, R. (1992). Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. *The Wilson Bulletin* 104(3): 400–412.
- Lefebvre, G., Poulin, B., & McNeil, R. (1994). Spatial and social behaviour of Nearctic warblers wintering in Venezuelan mangroves. *Canadian Journal of Zoology* 72: 757–764.
- Lemon, R. E., Weary, D. M. & Norris, K. J. (1992). Male morphology and behavior correlate with reproductive success in the American redstart (*Setophaga ruticilla*). *Behavioral Ecology and Sociobiology* 29: 399–403.
- Lenda, M., Maciusik, B., & Skórka, P. (2012). The evolutionary, ecological and behavioural consequences of the presence of floaters in bird populations. *North-Western Journal of Zoology* 8(2): 394–408.
- Lin, C.W., Hsu, F.H., & Ding, T.S. (2011). Applying a territory mapping method to census the breeding bird community composition in a montane forest of Taiwan. *Journal of Forest Science* 26(3): 267–285.
- Lobón-Cerviá, J. (2010). Density dependence constrains mean growth rate while enhancing individual size variation in stream salmonids. *Oecologia* 164: 109–115.
- López-López, P., Garcia-Ripolles, C., & Urios, V. (2014). Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecological Applications* 24(5): 938–949.
- López-Sepulcre, A., & Kokko, H. (2005). Territorial defense, territory size, and population regulation. *The American Naturalist* 166(3): 317–29.
- Lyons, J. E., Royle, J. A., Thomas, S. M., Elliott-Smith, E., Evenson, J. R., Kelly, E. G., & Andres, B. A. (2012). Large-scale monitoring of shorebird populations using count data and N-mixture models: Black Oystercatcher (*Haematopus bachmani*) surveys by land and sea. *The Auk* 129(4): 645–652.
- Mallord, J.W., Dolman, P.M., Brown, A. and W.J. Sutherland. (2007). Quantifying density-dependence in a bird population using human disturbance. *Oecologia* 153:49–56
- Marra, P. P. (1998). Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science* 282(5395): 1884–1886.

- Marra, P. P., & Holberton, R. L. (1998). Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116(1-2): 284–292.
- Marra, P. P. (2000). The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11(3): 299–308.
- Marra, P., & Holmes, R. (2001). Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *The Auk* 118(1): 92–104.
- Marra, P., Sherry, T., & Holmes, R. (1993). Territorial Exclusion by a long-distance migrant warbler in Jamaica : a removal experiment with American Redstarts (*Setophaga ruticilla*). *The Auk* 110(3): 565–572.
- Marra, P.P., Studds, C.E., Wilson, S., Sillett, T.S. Sherry, T.W., & Holmes, R.T. (in review) Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proceedings of the Royal Society- London*.
- McKellar, A. E., Marra, P. P., Hannon, S. J., Studds, C. E., & Ratcliffe, L. M. (2014). Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* 172(2): 595–605.
- Meir, P. & Pennington, R.T. (2011). Climatic change and seasonally dry tropical forests. Pages 279-299 in Seasonally dry tropical forests: ecology and conservation. R. Dirzo, H.S. Young, H.A. Mooney, and G. Ceballos [editors]. Island Press, Washington, D.C., USA
- Miller, T.E.X. (2007). Demographic models reveal the shape of density dependence for a specialist insect herbivore on variable host plants. *Journal of Animal Ecology* 76: 722-729.
- Millennium Ecosystem Assessment. (2005). Ecosystems and Human Well-being: Synthesis (pp. 1–155). Island Press, Washington D.C.
- Morschhauser, T., Rudolf, K., Botta-Dukat, Z., & Oborny, B. (2009). Density-dependence in the establishment of juvenile *Allium ursinum* individuals in a monodominant stand of conspecific adults. *Acta Oecologia* 35: 621-629.
- Morton, G., Lynch, J.F., Young, K., & Mehlhop, P. (1987). Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? *The Auk* 104: 133–135.
- Muller, K., Stamps, J., Krishnan, V., & Willits, N. (1997). The Effects of Conspecific Attraction and Habitat Quality on Habitat Selection in Territorial Birds. *The American Naturalist* 150(5): 650–661.
- Murdoch, W. (1994). Population regulation in theory and practice. *Ecology* 75(2): 271–278.
- Neelin J.D., Munnich M., Su, H., Meyerson J.E., & Holloway, C.E. (2006). Tropical drying trends in global warming models and observations. *Proceedings of the National Academy of Sciences- USA* 103:6110-6115.
- Nevoux, M., Barbraud, J.-C., & Barbraud, C. (2008). Nonlinear impact of climate on survival in a migratory white stork population. *The Journal of Animal Ecology* 77(6): 1143–52.

- Nevoux, M., Gimenez, O., Arlt, D., Nicoll, M., Jones, C., & Norris, K. (2011). Population regulation of territorial species: both site dependence and interference mechanisms matter. *Proceedings. Biological Sciences / The Royal Society* 278(1715): 2173–2181.
- Newbold, T., Hudson, L. N., Phillips, H. R. P., Hill, S. L. L., Contu, S., Lysenko, I., & Purvis, A. (2014). A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society of London Series B: Biological Sciences* 281: 20141371.
- Newman, M. E., McLaren, K. P., & Wilson, B. S. (2014). Long-term socio-economic and spatial pattern drivers of land cover change in a Caribbean tropical moist forest, the Cockpit Country, Jamaica. *Agriculture, Ecosystems & Environment* 186: 185–200.
- Newton, I. (1998). Population limitation in birds. Academic Press, California.
- Newton, I. (2004). Population limitation in migrants. *Ibis* 146(2): 197–226.
- Norris, D., Marra, P., & Bowen, G. (2006). Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). *Ornithological Monographs* (61): 14–28.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings. Biological Sciences / The Royal Society* 271(1534): 59–64.
- North American Bird Conservation Initiative, U. C. (2014). *The State of the Birds. 2014* (pp. 1–9).
- Ntiama-Baidu, Y., Nuoh, A. A., Reneerkens, J., & Piersma, T. (2014). Population Increases in Non-Breeding Sanderlings in Ghana Indicate Site Preference. *Ardea* 102(2): 131–138.
- Ockendon, N., Johnston, A., & Baillie, S. R. (2014a). Rainfall on wintering grounds affects population change in many species of Afro-Palaeartic migrants. *Journal of Ornithology* 155: 905–917.
- Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., & Pearce-Higgins, J. W. (2014b). Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology* 20(7): 2221–2229.
- Oro, D., Pradel, R., & Jimenez, J. (2004) Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *Journal of Animal Ecology* 73: 723–736.
- Parrish, J. & Sherry, T. (1994). Sexual habitat segregation of American Redstarts wintering in Jamaica: Importance of resource seasonality. *The Auk* 111(1): 38–49.
- Pearce-Higgins, J.W., Yalden, D.W., Dougall, T.W., & Beale, C.M. (2009). Does climate change explain the decline of a trans-Saharan Afro-Palaeartic migrant? *Oecologia* 159: 649–659.
- Penteriani, V., Ferrer, M., & Delgado, M. M. (2011). Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of non-breeders in avian populations. *Animal Conservation* 14(3): 233–241.
- Penteriani, V., Ojalora, F., & Ferrer, M. (2005). Floater survival affects population persistence- the role of prey availability and environmental stochasticity. *Oikos* 108(3): 523–534.

- Petit, D. R., Lynch, J.F., Hutto, R.L., Blake, J.G., & Waide, R.B. (1995). Habitat use and conservation in the Neotropics, p. 145–197. In T. E. Martin and D. M. Finch [Eds.], *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York.
- Pidgeon, A. M., Radeloff, V. C., & Mathews, N. E. (2006). Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*). *Biological Conservation* 132(2): 199–210.
- Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L., & Sauer, J. R. (2002). Large-scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13(2): 105–119.
- Poulin, B., G. Lefebvre, & McNeil, R. (1992). Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295–2309.
- Pradel, R., Hines, K.E., Lebreton, J.D. & Nichols, J.D. (1997). Capture-recapture survival models taking account of transients. *Biometrics* 53: 60-72.
- Price, T. & Gross, S. 2005 Correlated evolution of ecological differences among the Old World leaf warblers in the breeding and non-breeding seasons. In *Birds of two worlds* (eds R. Greenberg & P. Marra), pp. 359–372. Washington, DC: Smithsonian Institution Press.
- Pulliam, H. R. & Danielson, B. J. (1991). Sources, Sinks, and Habitat Selection: A Landscape Perspective on Population Dynamics. *The American Naturalist* 137: S50-S66.
- Pulliam, H. R., Dunning, John B., J., & Liu, J. (1992). Population Dynamics in Complex Landscapes : A Case Study. *Ecological Applications* 2(2): 165–177.
- Pyle, P. (1997). Identification guide to North American birds, Part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.
- Rappole, J.H., Ramos, M.A., & Winker, K. (1989). Movements and mortality in wintering Wood Thrushes. *The Auk* 106: 402–410.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Reed, T. E., Gienapp, P., & Visser, M. E. (2014). Density dependence and microevolution interactively determine effects of phenology mismatch on population dynamics. *Oikos* 124: 81–91.
- Reidy, J. L., Thompson, F. R., & Bailey, J. W. (2011). Comparison of methods for estimating density of forest songbirds from point counts. *The Journal of Wildlife Management* 75(3): 558–568.
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M., & Ratcliffe, L. M. (2009a). Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proceedings of the Royal Society, Biological Sciences* 276: 1619–26.
- Reudink, M. W., Studds, C. E., Marra, P. P., Kurt Kyser, T., & Ratcliffe, L. M. (2009b). Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. *Journal of Avian Biology* 40(1): 34–41.

- Robbins, C. S., Sauer, J. R., Greenberg, R. S., & Droege, S. (1989). Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences of the United States of America* 86(19): 7658–7662.
- Rockwell, S., Bocetti, C., & Marra, P. (2012). Carry-Over Effects of Winter Climate on Spring Arrival Date and Reproductive Success in an Endangered Migratory Bird, Kirtland's Warbler (*Setophaga kirtlandii*). *The Auk* 129(4): 744–752.
- Rodenhouse, N., Sherry, T., & Holmes, R. (1997). Site-dependent regulation of population size: a new synthesis. *Ecology* 78(7): 2025–2042.
- Rodenhouse, N. L., Sillett, T. S., Doran, P. J., & Holmes, R. T. (2003). Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings. Biological Sciences / The Royal Society* 270(1529): 2105–2110.
- Rosenzweig, M. (1991). Habitat Selection and Population Interactions : The Search for Mechanism. *The American Naturalist* 137(Supplement: Habitat Selection): S5–S28.
- Rotella, J.J., Link, W.A., Nichols, J.D., Hadley, G.L., Garrott, R.A., & Proffitt, K.M. (2009). An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals. *Ecology* 90(4): 975–984.
- Royle, J. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60(1): 108–115.
- Ruiz-Gutierrez, V., Kendall, W.L., Saracco, J.F., & White, G.C. (in review). Overwintering strategies of migratory birds: a novel approach for making inferences on movement patterns of residents and transients. *Journal of Applied Ecology*.
- Runge, M., & Marra, P. (2005). Modeling Seasonal Interactions in the Population Dynamics of Migratory Birds, p. 375–389. In R. Greenberg and P.P. Marra (Eds), *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, MD.
- Salewski, V. & Jones, P. (2006). Palearctic passerines in Afrotropical environments: a review. *Journal of Ornithology* 147:192–201.
- Scales, J., Hyman, J., & Hughes, M. (2013). Fortune favours the aggressive: territory quality and behavioural syndromes in song sparrows, *Melospiza melodia*. *Animal Behaviour* 85(2): 441–451.
- Schaub, M. & von Hirscheydt, J. (2009). Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture-recapture models. *Journal of Animal Ecology* 78: 625–635.
- Schmidt, J. H., McIntyre, C. L., & MacCluskie, M. C. (2013). Accounting for incomplete detection: What are we estimating and how might it affect long-term passerine monitoring programs? *Biological Conservation* 160: 130–139.
- Segura, A., Martínez, J., & Alcántara, M. (2012). Population Size of the Endangered Bearded Vulture *Gypaetus barbatus* in Aragon (Spain): An Approximation to the Pyrenean Population. *Ardeola* 59(1): 43–55.
- Sherry, T.W. & Holmes, R.T. (1992). Population Fluctuations in a Long-Distance Neotropical Migrant: Demographic Evidence for the importance of Breeding Season Events in the American Redstart. Pp.

- 431-442 in J.M. Hagan III and D.W. Johnston, eds. *Ecology and Conservation of Neotropical Migrant Landbirds*, Smithsonian Inst. Press, Wash., D.C.
- Sherry, T.W., & Holmes, R. (1996). Winter Habitat Quality, Population Limitation, and Conservation of Neotropical-Nearctic Migrant Birds. *Ecology* 77(1): 36–48.
- Sherry, T.W. & Holmes, R.T. (1997). American Redstart (*Setophaga ruticilla*). In *Birds of North America*, No. 277 (A. Poole and F. Gill, eds.). The academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; the American Ornithologists' Union, Washington, DC.
- Sherry, T.W., Wilson, D.S., Hunter, C.S. & Holmes, R. T. (2015). Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory bird. *Journal of Avian Biology*, accepted for publication 5 April, 2015.
- Sillett, T. S., Chandler, R. B., Royle, J. A., Kéry, M., & Morrison, S. A. (2012). Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications* 22(7): 1997–2006.
- Sillett, T.S. & Holmes, R.T. (2005). Long-term demographic trends, limiting factors, and the strength of density dependence in a breeding population of a migratory songbird. Pages 426-436 in R. Greenberg and P.P. Marra, [Eds.]. *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, MD, USA.
- Sillett, T. S., Holmes, R. T., & Sherry, T. W. (2000). Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288: 2040–2042.
- Sillett, T.S., Rodenhouse, N.L., & Holmes, R.T. (2004). Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85(9): 2467–2477.
- Sliwa, A. & Sherry, T. W. (1992). Surveying wintering warbler populations in Jamaica: point counts with and without broadcast vocalizations. *The Condor* 94(4): 924–936.
- Smith, J.A.M., Reitsma, L. R., & Marra, P. P. (2010). Moisture as a determinant of habitat quality for a nonbreeding neotropical migratory songbird. *Ecology* 91(10): 2874–2882.
- Smith, J. A. M., Reitsma, L. R., & Marra, P. P. (2011). Multiple space-use strategies and their divergent consequences in a nonbreeding migratory bird (*Parkesia noveboracensis*). *The Auk* 128(1): 53–60.
- Smith, K. G. & Rotenberry, J. T. (1990). Quantifying food resources in avian studies: present problems and future needs. *Studies in Avian Biology* 13:3-5.
- Sorensen, M. C., Hipfner, J. M., Kyser, T. K., & Norris, D. R. (2009). Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *The Journal of Animal Ecology* 78(2): 460–7.
- Soutullo, A., Limiñana, R., Urios, V., Surroca, M., & Gill, J. (2006). Density-dependent regulation of population size in colonial breeders: Allee and buffer effects in the migratory Montagu's harrier. *Oecologia* 149(3): 543–52.
- Staicer, C.A., V. Ingalls, & Sherry, T.W. 2006. Singing behavior varies with breeding status of American Redstarts (*Setophaga ruticilla*). *Wilson Journal of Ornithology* 118(4): 439-451.

- Stewart, S.R. (2005). Hurricane Ivan Tropical Cyclone Report. National Hurricane Center.
- Strong, A. M. & Sherry, T. W. (2001). Body Condition of Swainson's Warblers Wintering in Jamaica and the Conservation Value of Caribbean Dry Forests. *The Wilson Bulletin* 113(4): 410–418.
- Studds, C. & Marra, P. (2005). Nonbreeding habitat occupancy and population processes : an upgrade experiment with a migratory bird. *Ecology* 86(9): 2380–2385.
- Studds, C. & Marra, P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research* 35: 115–122.
- Studds, C. E. & Marra, P. P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings. Biological Sciences / The Royal Society*, 278(1723): 3437–43.
- Stutchbury, B. J. (1994). Competition for winter territories in a Neotropical migrant: the role of age, sex, and color. *Auk* 111: 63–69.
- Suarez-Rubio, M. & Thomlinson, J. R. (2009). Landscape and patch-level factors influence bird communities in an urbanized tropical island. *Biological Conservation* 142(7): 1311–1321.
- Sullivan, M.J.P., Newson, S.E., & Pearce-Higgins, J.W. (2015) Evidence for the buffer effect operating in multiple species at a national scale. *Biology Letters* 11: 20140930.
- Summers, R.W., Underhill, L.G., Howells, R.J., Vickery, J.A. & Prys-Jones, R.P. (1996). Phenology of migration and use of wintering sites by the increasing population of dark-bellied Brent geese, *Branta bernicla bernicla*. *Journal of Zoological London* 239: 197–208.
- Sutherland, W. (1996). Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London- Biological Sciences* 263(1375): 1325–1327.
- Sutherland, W. (1998). The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology* 35(3): 418–421.
- Sutherland, W. J. & Norris, K. (2002). Behavioural models of population growth rates: implications for conservation and prediction. *Phil. Trans. R. Soc. Lond. B* 357: 1273–1284.
- Terborgh, J. (1989). *Where Have All the Birds Gone?* Princeton University Press: Princeton, NJ.
- Tellería, J. & Pérez-Tris, J. (2003). Seasonal distribution of a migratory bird: effects of local and regional resource tracking. *Journal of Biogeography* 30:1583–1591.
- Thaxter, C. B., Joys, A. C., Gregory, R. D., Baillie, S. R., & Noble, D. G. (2010). Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation* 143(9): 2006–2019.
- Toms, J. D. (2011). Non-breeding competition between American redstarts (*Setophaga ruticilla*) and resident Adelaide's warbler (*Dendroica adelaidae*) in the Guanica Biosphere Reserve, Southwest Puerto Rico. PhD Dissertation, University of Missouri.
- Toms, J. D. (2013). Linking behavior and community ecology: interspecific aggression provides evidence for competition between a migrant and resident warbler. *Ethology* 119:1057–1066.

- Tonra C.M., Marra P.P., & Holberton R.L. (2011). Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. *Journal of Avian Biology* 42: 397–404.
- Townsend, J. & Rimmer, C. (2011). Sex and Age Ratios of Bicknell's Thrush Wintering in Hispaniola. *The Wilson Journal of Ornithology* 123(2): 367–372.
- Townsend, J., Rimmer, C., McFarland, K., & Goetz, J. (2012). Site-Specific Variation in Food Resources, Sex Ratios, and Body Condition of an Overwintering Migrant Songbird. *The Auk* 129(4): 683–690.
- Treberg, M.A. & Turkington, R. (2010). Density dependence in an experimental boreal forest understory community. *Botany* 88(8): 753–764.
- Turchin, P. (1999). Population Regulation : A Synthetic View. *Oikos* 84(1): 153–159.
- Utz, R.M. & Hartman, K.J. (2009). Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66(7): 1072–1080.
- Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management* 47(4): 893–901.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17(2): 76–83.
- Weis, T. (2000). Beyond peasant deforestation: environment and development in rural Jamaica. *Global Environmental Change* 10(4): 299–305.
- Wilson, J.R.U., Rees, M., & Ajuonu, O. (2006). Population regulation of a classical biological control agent: larval density dependence in *Neochetina eichhorniae* (Coleoptera: Curculionidae), a biological control agent of water hyacinth *Eichhornia crassipes*. *Bulletin of Entomological Research* 96: 145–152.
- Wilson, S., LaDeau, S. L., Tøttrup, A. P., & Marra, P. P. (2011). Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* 92(9): 1789–1798.
- Wilson, S., Marra, P. P., & Sillett, T. S. (2013). The effects of experimental irrigation on plant productivity, insect abundance and the non-breeding season performance of a migratory songbird. *PloS One* 8(1): 1–9.
- Winker, K. 1998. The concept of floater. *Ornitologia Neotropical* 9: 111–119.
- Winker, K., Rappole, J.H., & Ramos, M.A. (1995) The use of movement data as an assay of habitat quality. *Oecologia* 101: 211–216.
- Winker, K., J. H. Rappole, & Ramos, M.A. (1990). Population dynamics of the Wood Thrush in southern Veracruz, Mexico. *Condor* 92: 444–460.
- Wunderle Jr., J. (1995). Population Characteristics of Black-Throated Blue Warblers Wintering in Three Sites on Puerto Rico. *The Auk* 112(4): 931–946.

Wunderle, J. M. (1999). Avian Distribution in Dominican Shade Coffee Plantations: Area and Habitat Relationships. *Journal of Field Ornithology* 70(1): 58–70.

Biography

Ashley Marie Peele was born in Saint Cloud, Florida on May 26, 1985. Her childhood home sat on a large lake in what was a rural part of the county, so her childhood was spent exploring the swamps and oak woodlands of central Florida. This early exposure engendered a lasting love of the outdoors, which continues to influence her professional and personal interests. She graduated from Gateway High School with an International Baccalaureate Diploma in 2003 and went on to attend Ohio Wesleyan University, earning a Bachelor of Science in Zoology. During her freshman year, Ashley took an honors course in Avian Microbiology, which introduced her to the world of field biology. Her advising professor, Jed Burt, helped her to pursue a number of independent field research projects and jobs, including working on Mexican Spotted Owls in the Utah desert and collaborating with Smithsonian researchers to study pigment adaptations in subspecies of Swamp Sparrows. After graduating, Ashley worked for the Florida Cooperative Fish and Wildlife Research Unit at the University of Florida, studying the effects of lake management strategies on wildlife populations. In 2008, she joined Thomas W. Sherry's research lab at Tulane University as a PhD student and was co-advised by Peter Marra, Director of the Migratory Bird Center in the Smithsonian Conservation Biology Institute. She has taught Diversity of Life, General Ecology, and Ornithology laboratory courses at Tulane University, and looks forward to pursuing

teaching and research. Ashley currently lives in Asheville, North Carolina with her husband and hopes to continue working in her beloved Appalachians.