ABSTRACT

Title of Document:	ENVIRONMENTAL CONDITIONS IN WINTER AND THEIR ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES FOR AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*)
	Colin Eastman Studds, Doctor of Philosophy, 2008
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I used both observational and experimental approaches to assess the causes of

nonbreeding habitat quality and to evaluate their ecological and evolutionary

consequences for a Neotropical-Nearctic migratory bird, the American redstart

(*Setophaga ruticilla*). Relative to control birds overwintering in second-growth scrub,

redstarts experimentally upgraded from scrub to mangrove forest incorporated mangrove

stable-carbon isotope signatures, maintained mass over winter, departed earlier on spring

migration, and had higher apparent annual survival. Significantly higher arthropod

biomass on upgrade territories implicated food availability as a proximate mechanism of

habitat quality. Food availability, body condition, and spring departure schedules also

depended on nonbreeding season rainfall. Food availability in mangrove was higher than

in scrub in three of four years, allowing birds in this habitat to maintain superior body

condition and depart earlier on spring migration. Abundant rainfall in a single year led to

abnormally high food availability in scrub and early departure of birds in both habitats, suggesting both the amount and timing of rainfall influenced nonbreeding performance. Habitat occupancy and annual variation in rainfall had significant consequences for natal dispersal and selection through annual survival. Stable-hydrogen isotope ratios (δD) in feathers of immature birds captured again as adults indicated that habitat use in the first nonbreeding season interacted with spring phenology on temperate breeding grounds to influence the distance traveled on the first spring migration and direction of natal dispersal. In contrast, adults showed site fidelity between breeding seasons, suggesting nonbreeding conditions did not affect breeding dispersal and that migration distance becomes fixed later in life. Patterns of δD also revealed directional selection for short migration distance to southern breeding areas, a pattern that was nearly twice as strong in scrub compared to mangrove. During dry winters, redstarts experienced stabilizing selection on departure dates and directional selection for short migration. In years of high rainfall, birds experienced correlational selection favoring late departure when in good body condition. Thus, occupancy of moist habitats and years of high rainfall relaxed selection against late departure and longer migration. Collectively, these findings emphasize the need to understand how events throughout the annual cycle interact to shape fundamental biological processes.

ENVIRONMENTAL CONDITIONS IN WINTER AND THEIR ECOLOGICAL
AND EVOLUTIONARY CONSEQUENCES FOR AMERICAN REDSTARTS
(*SETOPHAGA RUTICILLA*)

By

Colin Eastman Studds

Dissertation submitted to the Faculty of the Graduate School of the
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Preface

The first three chapters of this dissertation have been published, in order, in the journals *Ecology*, *Climate Research*, and *Proceedings of the National Academy of Sciences of the United States of America*. Each journal has granted me permission to reproduce copyrighted material.

All research was conducted in accordance with permits issued by the Jamaica National Environment and Planning Agency, the U. S. Department of Agriculture, the U.S. Fish and Wildlife Service, and protocols approved by the Institutional Animal Care and Use Committees of the Smithsonian National Zoological Park and the University of Maryland.

Dedication

This dissertation is dedicated to my fiancé Rina Aviram. This work would not have

been possible without her love and friendship.

Acknowledgements

The co-chairs of my dissertation committee, David Inouye and Peter Marra, helped me to grow as both a scientist and a person. David Inouye provided generous guidance during all phases of my work. Peter Marra became everything I had hoped for in an advisor: a mentor, a sounding board, a collaborator and ,most importantly, a friend. I also thank other members of my committee, Michele Dudash, Doug Gill, Dan Gruner, and Charlie Mitter, for their advice and insight. The students and post-docs of the BEES program and the Smithsonian Migratory Bird Center have been excellent friends and colleagues, particularly Barbara Ballentine, Bill DeLuca, and Nora Diggs.

I worked with a group of outstanding field assistants in Jamaica: Traynor Biasiolli, Krista Cramer, Herlitz Davis, Melissa Evans, Nick Friedman, Peter Goulet, Jennifer Greenwood, Quentin Hays, Emily Klein, Matthew Reudink, Khara Strum, Chris Tonra, and Brett Tryon. David Brown and I did our field research alongside one another for three years. Our brainstorming, cooperation, and laughter were invaluable. Nuff respect to Sadie Gordon, Mackie Gordon, Ann Lyons, Andrew Williams, and Tracey Hawthorne. Their friendship and hospitality helped make Jamaica a second home to me.

Rina Aviram, Michele Dudash, Russ Greenberg, David Inouye, Shannon LaDeau, Kathryn Langin, Steve Latta, Ryan Norris, Matthew Reudink, Mark Schwartz, Scott Sillett, and Jeff Walters improved this work through discussions and comments on previous drafts.

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Overview

Neotropical-Nearctic migratory birds move between geographically distant habitats in response to seasonally changing conditions, a process that involves considerable challenges. During migration, individuals must negotiate novel habitats while making substantial physiological and energetic adjustments as they alternate between feeding at stopover sites and fasting en route. Once birds arrive on breeding or overwintering grounds, they encounter unique prey and distinct plant and animal communities, forcing them to cope with a shifting profile of resources and species interactions as they attempt to grow, reproduce and survive. The variety and complexity of these processes, coupled with the broad spatial scale over which they occur, makes identification of limiting factors for migratory birds exceptionally difficult.

Early research on temperate breeding areas implicated habitat loss and fragmentation as the primary cause of population limitation. Equally compelling work suggested that migratory birds were limited by events during migration or by conditions on tropical winter areas. There is now general consensus that factors during one phase of the annual cycle are, by themselves, insufficient to explain year-round population process. The emerging view is that population limitation in migratory birds results from seasonal interactions that occur when performance in one phase of the annual cycle carries over to affect performance in a future phase.

The overarching goal of this research was to assess the role of food availability as the proximate mechanism underlying differences in habitat quality for American redstarts (*Setophaga ruticilla*) during their nonbreeding season in Jamaica

and to test new hypotheses about how conditions in this part of year influence ecological and evolutionary processes later on in the annual cycle. Redstarts are common throughout their nonbreeding range in the Caribbean, Central America, and northern South American. Both males and females are territorial during the tropical winter period and subsist exclusively on a diet of insects. However, adult males are dominant over females and some immature males, and exclude them from higher-quality habitats, which may contain superior food resources.

The dissertation is organized into two sections, each comprising two chapters. The first two chapters describe observational and experimental approaches used to understand how seasonal and annual variation in food availability influences redstart body condition and the timing of departure on spring migration. The other two chapters describe how these measures of performance contribute to two important aspects of life-history: natal dispersal and annual survival. Several critical inferences from this research were made possible by novel application of stable-carbon and hydrogen isotopes to verify habitat use within the nonbreeding period and to link individuals to geographic locations on their temperate breeding grounds in North America.

In **chapter 1**, I permanently removed behaviorally dominant males from high quality black mangrove forest, providing territory vacancies that subordinate females and immature males from nearby, lower-quality scrub then colonized. Stable-carbon isotope profiles of birds that moved from scrub to mangrove habitat provided confirmation that the manipulation was successful in providing access to a mangrove-based food web. Relative to controls that spent the winter in scrub habitat, these

individuals maintained or gained body mass, departed earlier on spring migration and had higher apparent annual survival. The availability of arthropods consumed as prey was nearly five times greater in mangrove compared to scrub, suggesting food availability as a proximate mechanism of bird performance in the nonbreeding period.
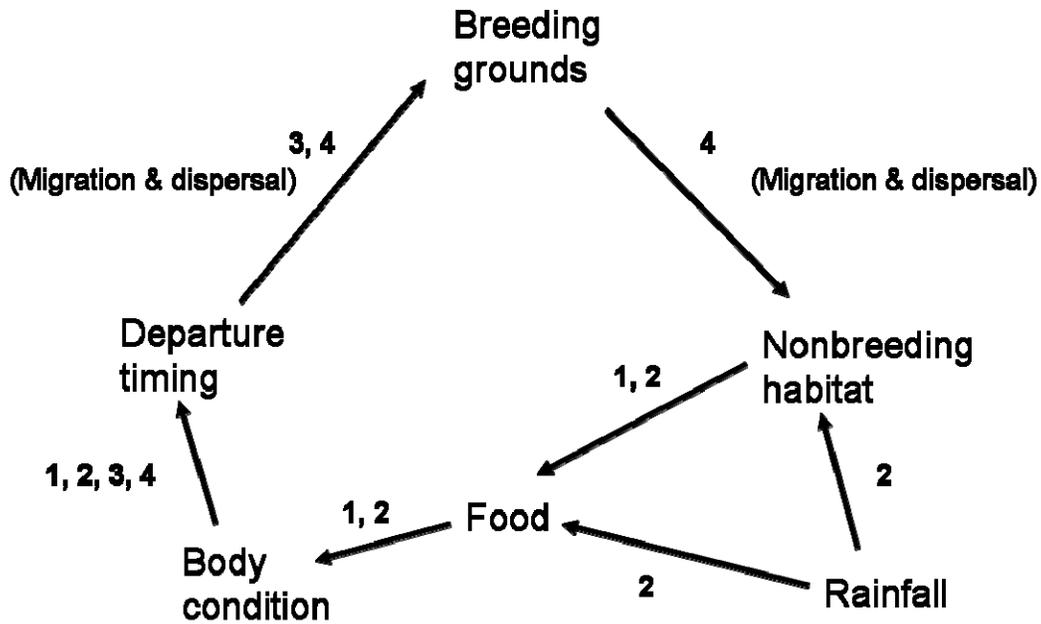
Schematic diagram of the relationships treated in this dissertation. Numbers near arrows refer to dissertation chapters addressing the relationship

In **chapter 2,** I examined how annual variation in rainfall during the nonbreeding season influenced food availability for redstarts and assessed its effect on body condition and spring migration schedules. Food availability and body condition of redstarts in both mangrove and scrub habitat varied in parallel with rainfall. In three of four years, food availability was higher in mangrove compared to scrub, permitting birds in this habitat to remain in superior body condition and depart earlier on migration. However, during a single year with uncommonly high rainfall in late

spring, food availability in scrub nearly equaled that in mangrove, allowing birds in both habitats to remain in good body condition and to leave on spring migration at roughly the same time. These data illustrated that both the timing and absolute amount of rainfall during the nonbreeding period can influence migratory departure schedules. The patterns of rainfall observed in this study occurred against a background of long-term decline in precipitation in Jamaica and lower rainfall in the Caribbean region is predicted as a consequence of changing climate. Thus, these findings provided insight about how migration schedules could shift in concert with changing rainfall.

In **chapter 3**, I addressed how the ecological conditions that vary between mangrove and scrub habitat contribute to patterns of natal dispersal. In many animals, natal dispersal involves a roughly linear movement from the natal site to the site of first breeding. However, long-distance migratory birds move directly from their natal territory to a tropical nonbreeding location, thus the process of natal dispersal is not complete until the conclusion of spring migration. Regardless of sex, immature redstarts occupying mangrove habitat during their first nonbreeding season maintained body mass over winter and departed early on migration. Stable-hydrogen isotopes in tail feathers grown at the natal site but sampled in winter revealed that early departing birds from mangrove made their first breeding attempt in southern parts of the breeding range and thus, on average, dispersed south of the latitude at which they fledged. In contrast, immature redstarts in scrub lost mass, departed later on migration, and made their first breeding attempt in more northern parts of the breeding range. As a consequence, these individuals dispersed to breed at a latitude

north of their natal site. Lilac bud-burst dates, a reliable indictor of emergence of arthropods and other plants, suggested that settlement of the first breeding attempt was influenced by phenology encountered upon arrival. Importantly, isotopic profiles of adult redstarts indicated substantial between-year fidelity to breeding areas, suggesting that redstarts may return for the remainder of their life to the same geographic area in which they first breed. These findings are the first to demonstrate that natal dispersal in a migratory animal can occur through an interaction between environmental conditions at temperate and tropical latitudes.

In **chapter 4** I asked how selection through annual survival in adult redstarts acts on three traits whose functional relationships were revealed through the research described in the three previous chapters: body condition, the timing of departure on spring migration, and migration distance as measured through stable-hydrogen isotopes. I compared the strength and form of selection acting between mangrove and scrub habitat and between pairs of years that varied in rainfall. I found that directional selection for short migration distance existed in both habitats, but was nearly twice as strong in scrub. In years of low rainfall, birds experienced both directional selection for shorter migration and stabilizing selection on departure date. In years of high rainfall, directional selection was comparatively weak and there was no evidence for stabilizing selection. Instead, correlational selection favored delayed departure on migration by birds in good body condition. These findings have important implications for the design of studies aimed at understanding how migration schedules may shift in relation to changing climate. Such research typically considers only how changing temperatures on breeding areas may alter

migration timing. However, failure to account for selective agents such as rainfall on the nonbreeding quarters could lead to researchers to overestimate the importance of temperature in driving phenotypic plasticity or evolution of migration timing.

The research outlined here and reported in detail in the following chapters emphasizes the need to study the ecology and evolution of migratory animals in a year-round context. It also suggests exciting new avenues of research that could yield important insights for both basic science and conservation.

Chapter 1: Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird[1]

Abstract.   Evidence is accumulating that winter habitats occupied by migratory birds produce differences in individual condition that can carry over into subsequent stages of the annual cycle. Despite strong observational evidence, experimental work is needed to strengthen support for this hypothesis. We experimentally upgraded individual American redstarts (*Setophaga ruticilla*) from low quality second-growth scrub habitat to high quality mangrove forest habitat by permanently removing behaviorally dominant, primarily adult males from mangrove, allowing females and immature males from scrub to colonize vacated territories. Prior to the manipulation, upgraded and control redstarts had stable-carbon isotope values in their blood indicative of scrub habitat occupancy, and were comparable in body mass. Relative to control birds that overwintered exclusively in scrub, upgraded redstarts incorporated mangrove isotopic signatures, maintained body mass from winter to spring, departed earlier on spring migration, and returned at a higher rate the following winter. Furthermore, arthropod biomass on upgrade territories was significantly greater than on control territories, suggesting food availability as a proximate mechanism underlying gradients of nonbreeding habitat suitability. Our findings demonstrate that winter habitat occupancy can be an important determinant of individual performance in migratory birds. Restricted access to food-rich winter

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habitats may limit survival of females and immature males, an outcome that could be an important driver of population structure and dynamics.

Introduction

Migratory animals move between geographically disparate habitats to meet seasonally changing needs, a process that may produce a suite of pressures on population dynamics. Nearctic-Neotropical migratory passerine birds spend three to four months on their temperate breeding grounds, about one to two months each on spring and fall migration, and six to seven months on their tropical winter quarters. Because of the spatially disjunct nature of these habitats and the difficulty of tracking individuals between seasons, contention remains about when population limitation occurs in the annual cycle (Rappole and McDonald 1994, Latta and Baltz 1997, Newton 2004). Much of the evidence for breeding season limitation comes from research on forest loss and fragmentation, including effects on food supply (Burke and Nol 1998, Zanette et al. 2000), nest predation and parasitism (Robinson et al. 1995, Rodewald and Yahner 2001), and annual survival (Bayne and Hobson 2002). Other evidence suggests migratory birds may be limited by events during migration (Moore et al. 1995, Sillett and Holmes 2002) or by food availability on tropical winter areas (Strong and Sherry 2000, Latta and Faaborg 2002).

A more holistic model for examining migratory bird population dynamics has emerged recently with the demonstration of carry-over effects (Marra et al. 1998, Gill et al. 2001, Møller et al. 2004, Norris et al. 2004a), which occur when ecological factors limit individual condition in one part of the annual cycle and thereby alter the timing or capacity of an individual to migrate, reproduce, or survive in a subsequent

stage (Runge and Marra 2005, Marra et al. 2006). Although recent work demonstrates that individuals with multiple failed nest attempts or that fledge offspring in late summer may delay molt until during fall migration (Norris et al. 2004b), most studies to date have examined carry-over effects originating during the winter portion of the annual cycle. Occupancy of poor quality winter habitats has been shown to affect physical condition adversely during migration (Bearhop et al. 2004), arrival date and condition at breeding sites (Marra et al. 1998, Gill et al. 2001), and reproductive success (Norris et al. 2004a). Elucidating how winter habitats determine individual performance and the process by which they produce carry-over effects therefore may be critical for understanding population dynamics of migratory birds.

In Jamaica, behaviorally dominant (predominantly adult male) American redstarts (*Setophaga ruticilla*), a Neotropical-Nearctic migratory bird, exclude subordinates (mostly females and immature males) from black mangrove forest, forcing them to occupy second-growth scrub habitat (Marra et al. 1993, Marra 2000). Long-term, observational data have shown that redstarts overwintering in mangrove, regardless of age or sex, maintain body mass throughout the winter period, depart earlier on spring migration, and have higher annual return rates compared to birds residing in scrub habitat (Marra et al. 1998, Marra and Holmes 2001). Although these findings strongly suggest that individual performance is determined by nonbreeding habitat occupancy, experimental work is needed to strengthen support for this hypothesis.

In 2002 and 2003, we experimentally upgraded primarily female and immature male redstarts from dry, second-growth scrub to mesic mangrove habitat. Previous removal experiments in this system were designed to test for floaters and mechanisms underlying sexual habitat segregation (Marra et al. 1993, Marra 2000). Research presented here builds upon this work, but differs in that we have not, until now, monitored the ecological consequences of these manipulations on individual performance.

To demonstrate that upgraded individuals originated from scrub and to confirm that they successfully persisted in mangrove territories, we measured stable-carbon isotopes signatures in blood, a reliable indicator of habitat occupancy (Marra et al. 1998), both before and after experimental upgrades. In addition, we sampled the availability of arthropods consumed as prey to assess the proximate mechanism underlying gradients of nonbreeding habitat suitability. We predicted that upgraded redstarts would develop stable-carbon isotope signatures to reflect mangrove habitat occupancy, maintain body mass over winter, depart earlier on spring migration, and return at a higher rate in the following year relative to control birds overwintering exclusively in scrub.

Methods

Our research was conducted on the southwestern coast of Jamaica at the Font Hill Nature Preserve (18°02'N, 77°57'), approximately 13 km west of Black River, St. Elizabeth Parish and 5 km east of Whitehouse, Westmoreland Parish. This area is one of the driest in Jamaica, with <1,000 mm of rain per year. The majority of

rainfall occurs between August and November, when monthly precipitation typically exceeds 100 mm. Rainfall declines to <25 mm per month after November, and by late February and early March drought conditions prevail throughout much of the area (Petroleum Corporation of Jamaica, unpublished data).

Redstarts were studied in two habitat types: coastal mangrove forest and second-growth scrub. Mangrove forest was dominated by black mangrove (*Avicennia germinans*), but also contained patches of white (*Laguncularia racemosa*) and red mangrove (*Rhizophora mangle*). Mangrove stands had a nearly continuous canopy averaging 12 m and little shrub and ground-level vegetation, except for mangrove pneumatophores, which grew to <20 cm. In early winter, mangrove trees were flooded with up to 1 m of water. Although water levels dropped with the onset of the dry season, pools of standing water remained through the spring, and mangroves retained their leaves, keeping this habitat comparatively shady and cool. Second-growth scrub was comprised mainly of logwood trees (*Haematoxylon campechianum*) but also had other species including *Bursera simarubra*, *Terminalia latifolia*, and *Crescentia alata*. Disturbance from cattle grazing and tree harvesting created a mosaic of vegetation types, with grassy fields in recently impacted areas and dense clusters of vines, shrubs, and trees with canopies ranging from 3−10 m in older sites. Unlike mangrove habitat, second-growth scrub never had standing water, and, as the dry season progressed, this habitat became increasingly arid, and most plants shed their leaves. Further description of the study area is available in (Marra and Holmes 2001).

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Six study sites were used: three 5 ha control sites consisting entirely of second-growth scrub and three 3 ha upgrade sites, which encompassed roughly 1.5 ha each of mangrove and scrub habitat. The transition between mangrove and scrub habitats at these sites was abrupt and could be accurately delineated by the upper extent of mangrove pneumatophore growth. The spatial proximity of scrub and mangrove habitats on the upgrade sites ensured that redstarts in scrub could monitor and exploit experimentally created vacancies in mangrove as soon as they were available. Upgrade sites were separated by >400 m, and were ≈500 m from the nearest scrub control site. The scrub control sites were >500 m from one another. All sites were flagged at 25-m intervals to facilitate locating and mapping redstart territories.

In winter (15 Jan–20 Feb) of 2002 and 2003, redstarts in control sites and in the scrub portion of upgrade sites were captured in mist nets, aged and sexed using criteria from Pyle (1997) and Marra et al. (1993), fitted with a unique color scheme of plastic leg bands and USFWS aluminum bands, measured for body size (bill dimensions, wing, tail and tarsus), weighed to the nearest 0.1 g, bled for stable-carbon isotope signatures, and released. Color-banded birds were followed and mapped for a minimum of three person-hours. Within a day of completing mapping observations, all behaviorally dominant, primarily adult male redstarts residing on the 1.5 ha mangrove section of upgrade sites were captured and sacrificed by thoracic compression. In this way, we created vacant mangrove territories, providing the opportunity for redstarts from scrub to upgrade to mangrove habitat.

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In spring (20 Mar–15Apr) of 2002 and 2003, after the onset of the winter dry season, we attempted to recapture, reweigh, and take a second blood sample for all upgraded and control birds. Beginning 1 April of each year, we resighted all upgraded and control individuals at 3-day intervals to determine the timing of migratory departure. When observers failed to resight a bird, its territory was visited twice more during that 3-day period, and then once again in the next 3-day period using a song-chip playback to confirm departure. In 2003 and 2004, we conducted intensive resight and recapture efforts to determine the number of control and upgrade birds that returned from the previous winter.

The availability of arthropods consumed as prey was measured on upgrade and control territories in winter (15 Jan–20 Feb) and again in spring (20 Mar–15 Apr) on territories of all recaptured birds. One observer made 20 passes of a sweep net over green vegetation while walking a circular route through the territory. The sweep net was fastened to a 5-m extension pole, allowing arthropods to be sampled from within the foraging height range of redstarts. The contents of the sweep net were overturned into a plastic bag and placed overnight in a freezer (-10°C). Arthropods were then preserved in 70 percent ethanol, dried at 50°C for 24 hours. All arthropods greater than 2 mm in length that are typically found in regurgitation and fecal samples (Sherry and Holmes 1997) were then weighed ($\pm$ 0.1 mg).

Blood samples were kept on ice in the field and centrifuged to separate plasma and hematocrit components. For isotope analysis, the hematocrit portion of each sample was freeze-dried, powdered, packaged in tin capsules, and weighed to the nearest 1μg. Samples were combusted in a Europa ANCA-GSL Elemental Analyzer

and introduced online into a Europa Hydra 20/20 Isotope Ratio Mass Spectrometer.

One in-house standard was run for every 6 unknowns. All analyses were done at the

University of California–Davis Stable Isotope Facility. Isotope values are expressed

in δ units relative to a Pee Dee belemnite standard where $\delta^{13}C = \{[(\delta^{13}C_{unk}/\delta^{12}C_{unk}) /$

$(\delta^{13}C_{std}/\delta^{12}C_{std})] \times 1000\}$. Samples were repeatable to within $\pm\ 0.2$ (mean $\pm\ 1$ SD)

part per mil ($n = 20$) based on repeated measurements of standards.

Data on stable-carbon isotope values, redstart body mass, and arthropod

biomass were examined using a repeated-measures mixed model with year (2002 and

2003) and treatment (upgraded and control redstarts) as main effects and time (pre-

and post upgrade) as the repeated measure. Wing length (unflattened wing chord)

was included in the model as a covariate to yield an estimate of mass corrected for

body size of each redstart. Individual bird nested within treatment was considered a

random effect. The relationship between overwinter body mass change and migratory

departure date was tested with ordinary least squares regression. Departure schedules

were analyzed with a Kaplan-Meier log-rank test. Return rate data were examined

with Pearson's chi-square test. All data met test assumptions, so no transformations

were used. Analyses were done with SAS 8.2 (SAS Institute 1999).

Results

In 2002 and 2003 combined, 28 redstarts were removed from their territories

in mangrove habitat (adult female: $n = 4$, yearling male: $n = 9$, adult male: $n = 15$).

Mapping observations indicated that 23 individuals shifted from second-growth scrub

habitat to experimentally vacated mangrove territories (yearling female: $n = 7$, adult

female: $n = 8$, yearling male: $n = 6$, adult male: $n = 2$). We also monitored 42

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redstarts in second-growth scrub control sites (yearling female: $n = 10$, adult female: $n = 22$, yearling male: $n = 2$, adult male: $n = 8$).

Stable-carbon isotope signatures in redstart blood differed between years (year: $F_{1, 19} = 33.15$, $P < 0.001$), but this difference was consistent between treatments (year $\times$ treatment: $F_{1, 19} = 0.74$, $P = 0.40$) and time periods (year $\times$ time: $F_{1, 20} = 0.58$, $P = 0.46$), so years were pooled. Stable-carbon isotope values in the blood of birds upgraded to mangrove were indistinguishable from those of control redstarts holding territories in scrub (controls: -23.88 $\pm$ 0.36 per mil SE; upgrades: -23.76 $\pm$ 0.37 per mil), confirming that upgraded individuals originated in scrub habitat. Two months after birds were upgraded, isotopic signatures late in the season were more depleted relative to controls (controls: -23.66 $\pm$ 0.36 per mil SE; upgrades: -25.95 $\pm$ 0.37; treatment $\times$ time: $F_{1, 20} = 20.76$, $P < 0.001$; Fig. 2A), confirming that upgraded redstarts successfully occupied mangrove territories and that control redstarts remained in scrub throughout the winter.

We found no evidence for annual variation in redstart body mass (year: $F_{1, 20} = 2.15$, $P = 0.16$). Control and upgraded redstarts did not differ in body mass prior to the manipulation (controls: 6.71 $\pm$ 0.05 g SE; upgrades: 6.78 $\pm$ 0.06 g), but diverged significantly following the manipulation (treatment $\times$ time: $F_{1, 22} = 7.54$, $P = 0.01$; Fig. 2B). On average, upgraded redstarts maintained body mass (6.80 $\pm$ 0.06 g), whereas birds in scrub controls lost up to 8% of early winter mass (6.52 $\pm$ 0.05 g).

Change in overwinter body mass was positively related to the timing of departure on spring migration ($r^2 = 0.20$, $P = 0.03$, $n = 25$). Upgraded redstarts departed their territories an average of 6 days ahead of control birds (Kaplan-Meier

log-rank test: $\chi^2 = 6.79$, $P = 0.009$; Fig. 3), a difference that was consistent between years (Kaplan-Meier log-rank test: $\chi^2 = 0.16$, $P = 0.69$).

Upgraded redstarts were also more likely to return the following winter compared to control birds in scrub ($\chi^2 = 4.63$, $P = 0.03$). Overall, 59% of experimentally upgraded redstarts were resighted on or nearby the mangrove territories they had occupied in the previous spring, whereas only 33% of redstarts that had overwintered in scrub were seen on study sites the following year.

Arthropod biomass was comparable in both years of the study (year: $F_{1, 19} = 0.15$, $P = 0.70$). Arthropod biomass was greater on upgrade compared to control territories immediately following the manipulation in winter (controls: 5.64 ± 1.68 g SE; upgrades: 18.42 ± 1.74 g). Differences in arthropod biomass between treatments remained pronounced for the duration of the experiment (treatment: $F_{1, 20} = 47.71$, $P < 0.0001$; Fig. 4), and were larger in spring (controls: 3.51 ± 1.68 g SE; upgrades: 19.60 ± 1.74 g) compared to winter, although not significantly so (treatment $\times$ time: $F_{1, 22} = 3.46$, $P = 0.07$).

Discussion

Few examples exist where researchers have successfully transplanted or upgraded birds to new habitats (Komdeur et al. 1997). Our experimental upgrade of primarily female and immature male American redstarts from second-growth scrub to mangrove forest allowed us to demonstrate convincingly that habitat occupancy is a critical factor influencing individual performance measures within winter and annual return rates. Relative to control redstarts overwintering in scrub, birds experimentally upgraded to mesic, mangrove forest remained in stable physical condition throughout

the spring dry season, departed earlier for migration, and returned at a higher rate in the following winter.

Because migratory birds do not mate or breed during winter, the sole benefit of acquiring and defending territories is to access resources needed for maintenance and survival. Evidence to date suggests that food is the most likely resource for which migratory birds compete in winter (Sherry et al. 2005). Food availability has been convincingly linked to patterns of abundance (Johnson and Sherry 2001) and overwinter changes in physical condition (Strong and Sherry 2000, Latta and Faaborg 2002). Arthropod biomass during this study averaged over three times greater in mangrove forest compared to second-growth scrub, most likely due to the differences in vegetation structure that develop or become exacerbated during the late-winter dry season (Parrish and Sherry 1994). Mangrove forest retains most of its leaves during this period, while most plants in second-growth scrub drop their leaves. The more extensive foliage cover in mangrove likely provided both food and refugia for phytophagous arthropods that constitute much of redstart prey (Sherry and Holmes 1997, Bearhop et al. 2004). Such differences in food availability might account for the variation in springtime physical condition between upgraded and control redstarts.

All upgraded and control redstarts survived through the winter period, suggesting that experimentally induced differences in physical condition did not become limiting until late spring. Birds upgraded to mangrove, which maintained mass, were able to depart on migration in advance of second-growth scrub controls, which lost mass. Recent research suggests that disparities in physical condition and departure timing induced by differences in winter habitat occupancy may have

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important consequences in subsequent seasons. (Bearhop et al. 2004) demonstrated that migrating Black-throated blue warblers (*Dendroica caerulescens*) that overwintered in mesic habitats were in better condition than birds originating from more xeric locations. Other research on redstarts has shown that birds wintering in mesic sites, regardless of sex or age, arrived earlier on breeding grounds (Marra et al. 1998), and, as a result, fledged significantly more young than birds from more xeric winter habitats (Norris et al. 2004a). Collectively, these findings support the hypothesis that habitat-specific winter physical condition can carry over to subsequent phases of the annual cycle.

Capture-recapture analyses of long-term survival data show the resight probability for redstarts in this population to be >90% (Studds and Marra unpublished data), evidence that the annual return rates reported here are likely a good indicator of true survival. However, because no analytical method can account for permanent dispersal, we acknowledge that at least some birds that failed to return to their territories the following year may have survived and wintered in other locations. Nonetheless, the notion that habitat-specific physical condition in winter may ultimately limit survival is important because, when applied to females, it suggests a mechanism by which density-dependent effects could regulate populations (Sherry and Holmes 1995, Runge and Marra 2005). Poor survival of females forced to winter in drought-prone environments like the second-growth scrub habitat studied here could lead to density-dependent feedback on per capita reproduction the following breeding season. Surplus female offspring might then be forced into low quality

habitats in the following winter, where they would experience disproportionately lower survival (Sherry and Holmes 1995).

Understanding how different periods of the annual cycle interact to drive sex ratio dynamics and density-dependent responses such as we have described above will require much additional research. First, it will be necessary to improve our knowledge of how variation in physical condition and survival operate in phases of the annual cycle other than winter. Second, it will be necessary to enhance our understanding of migratory connectivity (Webster et al. 2002, Marra et al. 2006) so that interactions between population size and demographic rates at different stages of the annual cycle can be examined between appropriate breeding and nonbreeding areas. Such advances will increase our understanding of how populations of migratory animals are regulated and will set the stage for collaborative conservation partnerships between researchers and managers at temperate and tropical latitudes.

Figure 2. (A) Stable carbon-isotope values (means ± 1 SE) in blood of control American redstarts occupying second-growth scrub (filled circles) and redstarts experimentally upgraded to mangrove habitat (open circles). (B) Corrected body mass (mass corrected for wing size; means ± 1 SE) of control (filled circles) and upgraded (open circles) redstarts. Blood was sampled and body mass measured immediately prior to the manipulation in winter (pre-upgrade) and two months later in spring (post-upgrade) on the nonbreeding grounds in Jamaica, West Indies.
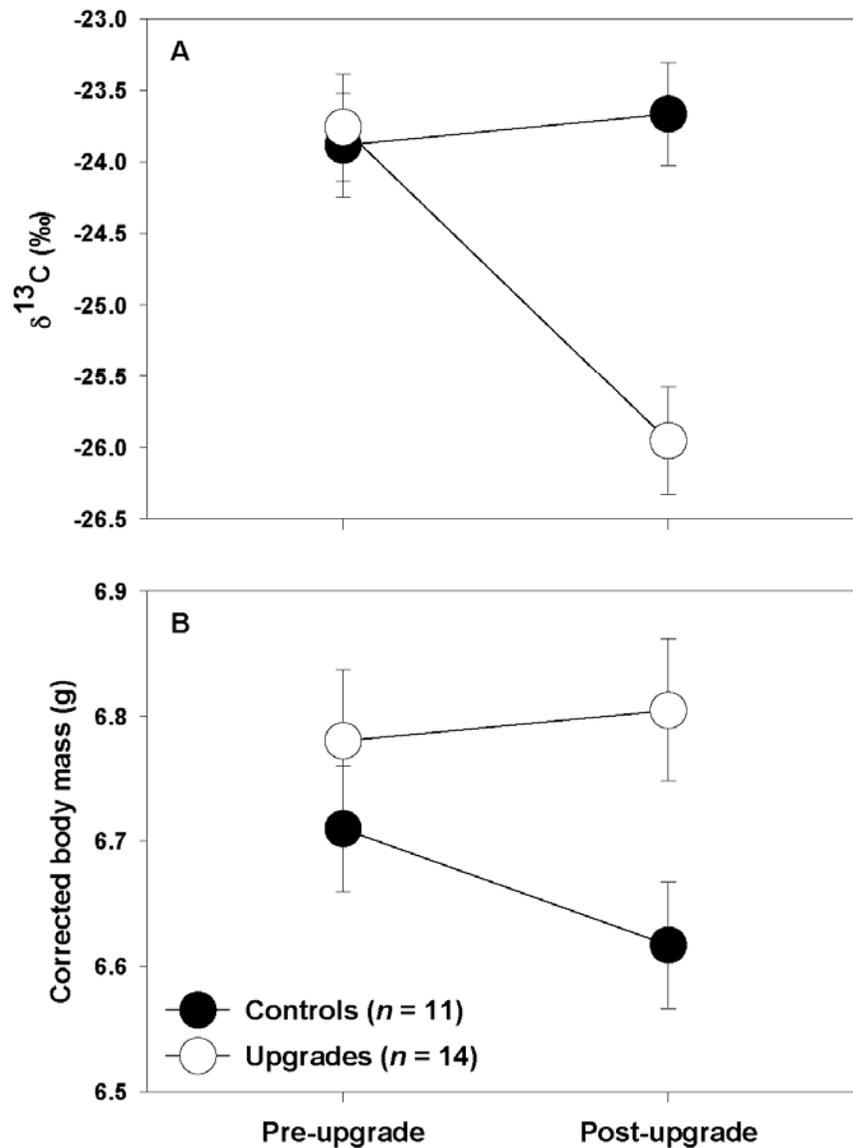
Figure 3. Spring migration departure schedules (means ± 1 SE) of control (filled circles) and upgraded (open circles) American redstarts from the nonbreeding grounds in Jamaica, West Indies.
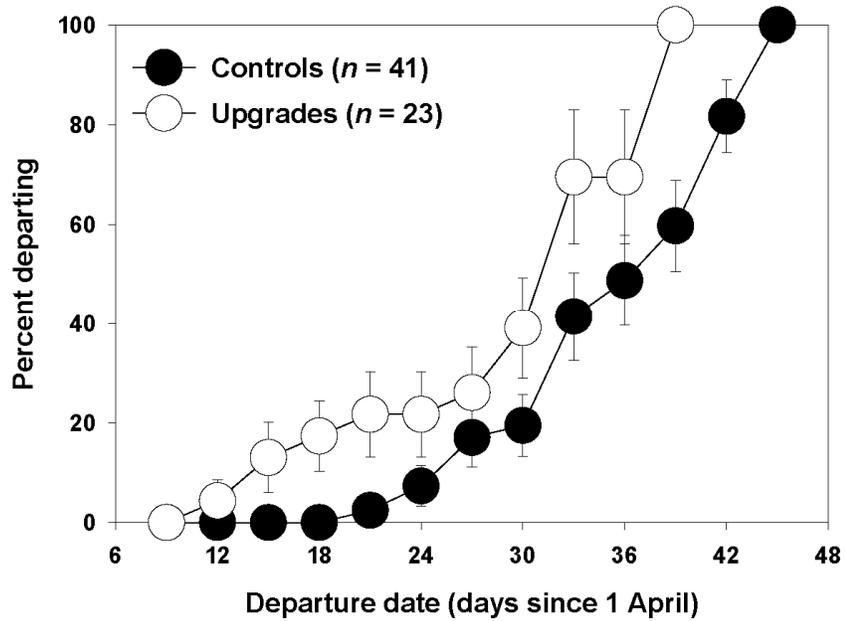
Figure 4. Biomass of arthropods (means ± 1 SE) available as prey on the territories of control (filled circles) and upgraded (open circles) American redstarts immediately following the manipulation in winter (pre-upgrade) and two months later in spring (post-upgrade) on the nonbreeding grounds in Jamaica, West Indies.
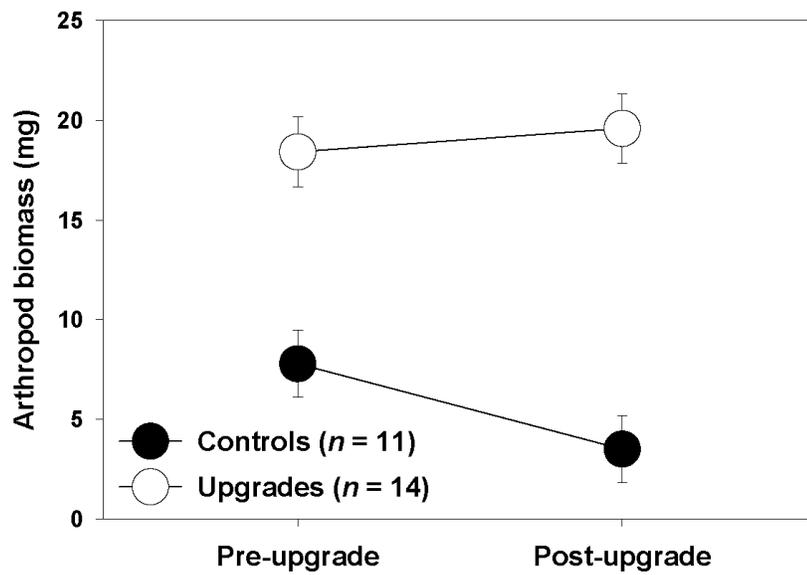
Chapter 2: Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird[2]

Abstract.   Research on long-distance migratory birds has yielded some of the strongest evidence that shifts in climate are changing ecosystem processes. Much of this work has focused on understanding whether rising temperatures on temperate breeding grounds are advancing migration phenology and limiting reproductive success. Conditions on tropical nonbreeding quarters, however, can also shape these processes, yet few studies have directly measured bird responses to climate during this part of the annual cycle. We tested the hypothesis that variation in winter rainfall can influence food availability and the nonbreeding season performance of American redstarts (*Setophaga ruticilla*) occupying two contrasting habitats: wet, mangrove forest and dry, second-growth scrub. From 2002–2005, food availability, body mass, and spring departure schedules of birds in both habitats were highly dependent on rainfall. Food availability in mangrove forest was higher than in second-growth scrub in three out of four years, allowing birds in this habitat to maintain better physical condition through the winter and depart earlier on spring migration. However, abundant rainfall in the spring of 2004 led to abnormally high food availability in scrub and early departure of birds in both habitats. These results suggest that rainfall on tropical wintering areas can have major effects on the nonbreeding season performance of migratory birds, and that the timing of rainfall within the dry season, not just the absolute amount, may be critical for orchestrating migratory departure

schedules. Because rainfall in some tropical regions is projected to decline drastically

over the next fifty years, migratory birds could face increasingly severe food

shortages prior to spring migration. Such conditions could force departure schedules

to become delayed and constrain adaptation to selection for earlier breeding in to

response rising temperatures on breeding areas.

Introduction

It is now clear that persistent shifts in climate are altering the structure and

function of ecosystems worldwide (Walther et al. 2002, Parmesan and Yohe 2003,

Root et al. 2003). Despite their astounding taxonomic diversity, many birds share

several life-history traits that have made them instrumental for evaluating the

consequences of changing climate: they are widely distributed, highly mobile, their

annual cycles hinge on seasonal phenological cues, and they have relatively short

generation times. Among the most prominent examples of such research are studies

measuring bird responses to rising temperatures along migratory routes or on

temperate breeding areas. Coincident with warming temperatures, many species in

both Europe and North America have advanced their breeding ground arrival dates

(Cotton 2003, Murphy-Klassen et al. 2005), begun breeding earlier (Crick et al. 1997,

Dunn and Winkler 1999), and extended their ranges poleward (Thomas and Lennon

1999, Hitch and Leberg 2007). In other species, arrival times at breeding areas have

remained unchanged as temperatures have increased (Mills 2005), or have not

advanced enough to remain in synch with changes in resource phenology at lower

trophic levels (Both and Visser 2001). The direction and magnitude of phenological

shifts have also been shown to vary across the breeding range for the same species

(Both et al. 2004, Both and te Marvelde 2007). This heterogeneity in response among species and regions suggests that temperature on breeding areas is not the only factor altering annual life cycle events of migratory birds. Trends toward earlier arrival and breeding time also could be caused by changes in departure schedules from the wintering grounds, or by changes in the pace of migration. For the latter there is considerable correlative data (Forchhammer et al. 2002, Marra et al. 2005, Hüppop and Winkel 2006), but whether departure dates from winter quarters are affected by climatic variables is largely unknown.

Substantial evidence suggests that rainfall during the nonbreeding season can have important consequences for migratory birds. Rainfall and temperature on the nonbreeding quarters in Africa has been shown to influence abundance, first arrival dates, and annual survival of birds on breeding areas in Europe (Møller 1989, Kanyamibwa et al. 1990, Peach et al. 1991, Szép 1995, Barbraud et al. 1999, Gordo et al. 2005). Indices of global climate cycles (e.g. ENSO), which correlate well with temporal rainfall dynamics, have also been linked to the annual survival of migratory birds wintering in the Caribbean (Sillett et al. 2000) and the breeding ground arrival schedules of birds spending the nonbreeding period in Africa (Cotton 2003). Recent advances in the application of remote sensing using the Normalized Difference Vegetation Index (NDVI) have broadened the scale and level of resolution with which ecological responses to precipitation can be examined (Pettorelli et al. 2005). Consistent with previous research, these studies find tight associations between NDVI data and breeding ground arrival time (Saino et al. 2004), annual survival (Szép and Møller 2005), and the onset of breeding (Both et al. 2006b).

Rainfall patterns stemming from broad-scale climate cycles can have direct and indirect effects on plant productivity (Oba et al. 2001, Nemani et al. 2003), arthropod abundance (Polis et al. 1997), and food plant quality for phytophagous arthropods (Huberty and Denno 2004), all of which may determine food availability for migratory birds. Multiple lines of evidence suggest that food is a key limiting factor for migratory birds during the nonbreeding period, particularly during the late-winter dry season (Sherry et al. 2005, Brown and Sherry 2006, Johnson et al. 2006). Late-winter dry seasons are commonplace in sub-equatorial regions and have been linked to seasonal declines in arthropod populations in tropical deciduous forests through both observations and experiments (Janzen 1973, Lefebvre et al. 1994, Parrish and Sherry 1994, Brown and Sherry 2006). The late winter dry season in many tropical locations is a critical time for migrants because of pre-migratory fattening (Brown & Sherry 2006), molt in some species (van den Brink et al. 2000), and the need to arrive at breeding areas in optimal condition and as early as possible (Marra et al. 1998, Norris et al. 2004a). To date, few studies have examined how rain and food on nonbreeding quarters interact to affect the physical condition and performance of migratory birds (Brown and Sherry 2006). Consequently, it is unclear how annual variation in nonbreeding season rainfall is likely to influence the timing of departure on spring migration.

Research on wintering populations of American redstarts (*Setophaga ruticilla*) in wet, mangrove forest and dry, second-growth scrub illustrates a tight linkage between moisture and bird performance. By the end of the winter dry season in Jamaica, the availability of arthropods consumed as prey is lower in second-growth

scrub than in mangrove forest (Studds and Marra 2005). This difference in food availability appears to affect multiple measures of redstart performance. Relative to redstarts occupying mangrove forest, birds in dry scrub have elevated corticosterone levels (Marra and Holberton 1998), lose mass over winter (Marra and Holmes 2001), depart later on spring migration (Marra et al. 1998, Studds and Marra 2005), and have lower annual survival (Johnson et al. 2006). Redstarts occupying dry winter habitats also arrive later on breeding areas, may be in poor physical condition upon arrival, and fledge fewer young compared to birds originating from wet locales (Marra et al. 1998, Norris et al. 2004a). Moisture gradients across these habitats, therefore, appear to drive food availability and, ultimately, the performance of American redstarts throughout their annual cycle. However, we have not, until now, examined how the habitat-specific performance of redstarts changes in response to annual variation in rainfall.

We tested the hypothesis that changes in rainfall across years can drive spatio-temporal variation in the nonbreeding season performance of American redstarts (Fig. 5). We predicted that differences in rainfall among years would lead to parallel variation in the abundance of arthropods available as prey, redstart physical condition, and the timing of departure on spring migration. Because mangrove forest retains standing water, we also predicted that birds in this habitat would be buffered from annual fluctuations in rainfall and food availability, allowing them to maintain superior physical condition and to depart earlier on spring migration relative to redstarts in second-growth scrub.

Methods

We conducted this research at the Font Hill Nature Preserve (18°02'N, 77°57'W, <5 m above sea level), about 13 km west of Black River, St. Elizabeth Parish, Jamaica. This area is one of the driest in Jamaica (<1,000 mm of rain per year), and, as is typical of many tropical regions, experiences strong seasonality in precipitation. Rainfall is high from August–November when average monthly rainfall typically exceeds 100 mm, and then usually declines to less than 25 mm per month during the dry season from January–March (Jamaica Meteorological Service, unpublished data).

Birds were studied in two habitat types: wet, mangrove forest and dry, second-growth scrub. Mangrove forest was dominated by black mangrove (*Avicennia germinans*), but also had some white (*Laguncularia racemosa*) and red mangrove (*Rhizophora mangle*). Trees in this habitat ranged from 8 to >75 cm diameter at breast height (dbh), were regularly distributed at intervals of 10–15 m, and had dense canopies averaging about 12 m in height. Mangrove stands were usually inundated with 0.5–1.0 m of standing water through January, but became progressively drier in February and March, drying out entirely in some years. Despite annual variation in surface water, mangrove trees retained the majority of their leaves during the dry season, keeping this habitat relatively cool and shady throughout the time when redstarts were present. Vegetation in second-growth scrub was dominated by logwood trees (*Haematoxylon campechianum*), a thorny species with a fluted trunk, but also contained several less common species, including *Bursera simarubra*, *Terminalia latifolia*, and *Crescentia alata*. Trees in this habitat were generally 2–8

cm dbh, grew from 3–10 m in height, and were interspersed with small, grassy fields and dense tangles of vines and shrubs. Unlike mangrove habitat, second-growth scrub never had standing water, and trees and other vegetation dropped most of their leaves during the dry season. Further description of the study area can be found in (Marra and Holmes 2001).

In spring (15 Mar–15 Apr) of 2002–2005, redstarts were captured in mist nets, aged and sexed using criteria from (Pyle 1997) and (Marra et al. 1993), fitted with a unique color scheme of plastic leg bands and USFWS aluminum bands, measured for body size, weighed to the nearest 0.1 g, and released. Redstart mass during this period reflects physical condition at the end of the late-winter dry season, when birds typically carry little or no visible subcutaneous fat. To delineate territory boundaries, we followed and mapped color-banded birds for a minimum of three person-hours spaced across at least one-month's time. From 1 April–15 May of each year, we resighted color-banded birds at 3-day intervals to determine their timing of departure on spring migration. When observers failed to resight a bird, its territory was visited twice more during that 3-day period, and then once again in the next 3-day period using a song-chip playback to confirm departure. To minimize the effect of time dependency of bird sampling, we captured redstarts in mangrove and scrub habitats on alternating days and monitored a roughly equal number of territories in each habitat during each 3-day interval of the spring departure period.

Arthropods available as redstart prey were measured in both habitats within two weeks of bird capture on a subset of territories. One observer made 20 passes of a sweep net over green vegetation while walking a circular route through the territory.

The sweep net was fastened to a 5-m extension pole, allowing arthropods to be sampled from within the foraging height range of redstarts. The contents of the sweep net were overturned into a plastic bag and placed overnight in a freezer (-10°C), preserved in 70 percent ethanol, and later dried at 50°C for 24 hours. All arthropods greater than 2 mm in length that are typically found in regurgitation and fecal samples (Sherry and Holmes 1997) were then weighed ($\pm$ 0.1 mg) to yield a single measure of food availability on each territory.

Local rainfall records were not available for all years of the study. We therefore obtained rainfall data from the Jamaica Meteorological Service for the Burnt Savannah climate monitoring station, approximately 10 km northwest of the study area.

Trends in January–March rainfall from 1995–2005 were analyzed with Pearson's correlation. We developed an estimate of redstart body mass corrected for the body size of each bird by first reducing data on unflattened wing chord, tarsus size, and tail length onto a single axis using principal components analysis (PCA). We then regressed body mass on the standardized factor scores from the PCA and used the residual values as an estimate of corrected body mass. Data on corrected body mass and arthropod biomass were examined using a general linear model (GLM) that included age, sex, and habitat occupancy as fixed effects, total rainfall from January–March of each year as a linear covariate, and all two-way interactions between demographic groups and environmental variables. We also included the Julian date of capture as a covariate in the analysis of corrected body mass to adjust for potential variation in redstart mass across the one-month capture period. The

relationship between corrected body mass and spring departure dates was evaluated

with ordinary least squares regression. We did not analyze spring departure

schedules from 2002 because birds were not monitored for the entire departure period

in this year. All data met the assumptions of parametric tests, so no transformations

were necessary. Analyses were done with SAS 8.2 (SAS Institute 1999)

Results

From 1995–2005, dry season rainfall (January–March) decreased by

approximately 17% ($r = 0.64$, $n = 11$, $P = 0.03$; Fig. 6). The timing of precipitation

also became more variable through time, as indicated by the increasing coefficient of

variation for rainfall within the dry season of each year ($r = 0.65$, $n = 11$, $P = 0.03$).

The increasing unpredictability of dry season precipitation is particularly evident in

recent years. For example, in 2004, 185 mm of rain fell across the entire dry season,

of which 108 mm came in March (Fig. 6), making this the second wettest spring since

1995. In contrast, 2005 was one of the driest years on record in Jamaica, with only 3

mm of rain in March.

During the dry seasons of 2002–2005, the biomass of arthropods available as

prey to American redstarts was greater in years of high rainfall in both mangrove

forest and second-growth scrub (GLM for rainfall: $F_{1, 51} = 4.96$, $P = 0.03$; for rainfall

× habitat: $F_{1, 51} = 2.00$, $P = 0.16$; Fig. 7). On average, redstarts in mangrove had

higher arthropod biomass on their territories compared to those in scrub (GLM for

habitat: $F_{1, 51} = 15.75$, $P = 0.0002$; Fig. 7). The variation in food availability between

habitats was pronounced in three out of four years (2002: 20.9 mg ± 2.8 in mangrove;

2.55 ± 3.00 in scrub; means ± 1 SE; 2003: 18.1 mg ± 3.0 in mangrove; 4.1 ± 2.6 in

scrub; 2005: 12.5 mg ± 1.9 in mangrove; 4.4 ± 2.4 in scrub). However, in the extremely wet spring of 2004 (Fig. 6), arthropod biomass in scrub was roughly equal to that in mangrove (18.2 mg ± 1.9 in mangrove; 18.8 ± 3.1 in scrub). These spatio-temporal differences in food availability held for all age- and sex-classes (GLM for age: $F_{1, 51} = 1.33$, $P = 0.25$; for age × rainfall: $F_{1, 51} = 0.00$, $P = 0.96$; for age × habitat: $F_{1, 51} = 1.74$, $P = 0.19$; for sex: $F_{1, 51} = 0.21$, $P = 0.65$; for sex × rainfall: $F_{1, 51} = 0.05$, $P = 0.82$; for sex × habitat: $F_{1, 51} = 0.08$, $P = 0.78$).

When corrected for their body size, the spring body mass of redstarts was higher in years of greater rainfall, an effect that was similar between habitats (GLM for rainfall: $F_{1, 214} = 20.80$, $P < 0.0001$; for rainfall × habitat: $F_{1, 214} = 1.20$, $P = 0.27$; Fig. 8). Birds overwintering in mangrove forest had higher corrected mass compared to those in second-growth scrub in all four years (GLM for habitat: $F_{1, 214} = 9.73$, $P = 0.002$; Fig. 8). These patterns of corrected body mass were not dependent on the date individual birds were captured (GLM for capture date: $F_{1, 214} = 2.06$, $P = 0.15$) and were consistent for all age- and sex-classes (GLM for age: $F_{1, 214} = 1.10$, $P = 0.30$; for age × rainfall: $F_{1, 214} = 0.01$, $P = 0.93$; for age × habitat: $F_{1, 214} = 1.50$, $P = 0.22$; for sex: $F_{1, 214} = 1.06$, $P = 0.31$; for sex × rainfall: $F_{1, 214} = 0.07$, $P = 0.79$; for sex × habitat: $F_{1, 214} = 0.19$, $P = 0.66$).

In 2003 and 2005, redstarts with higher corrected body mass departed earlier on spring migration compared to birds with lower mass (2003: $r^2 = 0.17$, $P = 0.02$, $n = 35$; 2005: $r^2 = 0.15$, $P = 0.03$, $n = 30$; Fig. 9). In these years, birds in mangrove forest left on migration before those in second-growth scrub (Kaplan-Meier log rank test for 2003: $\chi^2 = 7.55$, $P = 0.006$, $n = 35$; 29 ± 1 day since 1 April for mangrove; 36

± 1 day since 1 April for scrub; mean ± 1 SE; for 2005: habitat: $\chi^2 = 3.85$, $P = 0.04$, n = 30; 32 ± 2 days since 1 April for mangrove; 38 ± 2 days since 1 April for scrub). In contrast, corrected mass in 2004 was not a good predictor of spring departure schedules (2004: $r^2 = 0.01$, $P = 0.43$, $n = 47$; Fig. 9), and there was no difference in the timing of departure between habitats (Kaplan-Meier log rank test for 2004: $\chi^2 =$ 0.86, $P = 0.35$, $n = 47$; 30 ± 1 day since 1 April for mangrove; 30 ± 2 days since 1 April for scrub). When departure schedules from all three years were considered together, the average corrected body mass of all redstarts in each habitat was highly negatively correlated with the average date of departure on spring migration. ($r^2 =$ 0.86, $P = 0.001$, $n = 6$; Fig. 10).

Discussion

Previous research has demonstrated that nonbreeding season rainfall can have important consequences for the phenology of migration and the timing of reproduction in migratory birds (Sæther et al. 2004, Gordo et al. 2005, Both et al. 2006b, Saino et al. 2007). Such findings have led to the hypothesis that rainfall mediates the timing of departure on spring migration by influencing food availability for birds during the critical period of pre-migratory fueling (Forchhammer et al. 2002, Gordo et al. 2005). This idea has remained largely untested because few studies have directly measured rain-induced shifts in food supply and their consequences for nonbreeding season performance (Brown and Sherry 2006). Our results indicate that annual shifts in nonbreeding season rainfall determine food availability for redstarts during the late winter dry season, leading to marked differences in physical condition prior to migration, and, ultimately, to variation in spring departure schedules among

years. Food availability for redstarts changed not only with annual variation in rainfall, but also with spatial differences in habitat moisture. In three out of four years, food availability for birds in mangrove was higher, enabling them to maintain superior physical condition, and depart earlier on migration compared to birds in scrub.

The within-year relationships between spring body mass and the timing of departure on migration illustrate how temporal trends in rainfall and spatial gradients in habitat moisture can interact to shape spring departure schedules. In both 2003 and 2005, the body mass of individual redstarts at the end of dry season accurately predicted their migratory departure dates. Although total dry season rainfall in 2003 was over three times greater than in 2005, rainfall in March of both years was <20 mm. In these years, low March rainfall likely contributed to the marked differences in food availability between mangrove and scrub habitats, helping to drive the between-habitat variation in body mass and its significant influence on spring departure schedules. In contrast, although total dry season rainfall in 2003 and 2004 differed by <50 mm, over 100 mm of rainfall occurred in March 2004. Food availability in second-growth scrub and the body mass of birds in this habitat were higher following this rain pulse than at any other time during the study. Although redstart body mass in mangrove remained higher compared to birds in scrub, departure schedules in 2004 did not differ between habitats, and the relationship between body mass and the timing of departure was negligible. These results indicate that the timing of rainfall within the dry season, not just the absolute amount, may be

critical for orchestrating migratory departure schedules of birds in drought-prone environments.

The quality of nonbreeding habitat can have important implications for the future reproductive success of migratory birds. Individuals wintering in high quality habitats may arrive earlier at breeding sites and be in better physical condition compared to later arrivals (Marra et al. 1998, Gill et al. 2001). Delays in arrival of only a few days can reduce reproductive output by limiting the time available to replace failed clutches (Norris et al. 2004a) or by preventing access to high quality breeding habitat (Gunnarsson et al. 2006). The strong correlation we detected between the average body mass of redstarts at the end of the winter dry season and their average departure schedules in each year implies that the intensity of such carry-over effects could vary through time at individual nonbreeding sites or across spatial gradients in moisture at local and potentially regional scales. Because females predominate in dry, second-growth scrub (Marra and Holmes 2001), carry-over effects following dry springs are likely to be more severe for this sex. Variation in nonbreeding season rainfall could also be of particular concern for species with small populations or restricted winter distributions, especially if drought-induced carry-over effects exacerbate other limiting factors on breeding areas.

Knowledge of the factors that shape the timing of departure from nonbreeding quarters may also be important for predicting how changing climate could alter the phenology of spring migration. When considered in the context of long-term trends in winter rainfall, our results suggest that conditions experienced by redstarts during their nonbreeding season could constrain adaptive responses to selection for earlier

breeding that may result from rising temperatures on breeding areas. Over the past eleven years, rainfall at our Jamaican study sites has declined by approximately 17%. Moreover, consensus predictions from multiple models project drastic declines in rainfall throughout the Caribbean over the next fifty years (Neelin et al. 2006). Because food availability appears dependent on rainfall, birds may face increasingly greater food limitation during the critical period of pre-migratory fueling, leading to progressively greater delays in the timing of departure on spring migration. Under this scenario, redstarts would be unable to respond to selection for earlier breeding by advancing their spring departure dates. Selection pressures imposed by extreme drought on nonbreeding areas could also compound the ability of some birds to complete their migration successfully. Preliminary data for redstarts indicates that the annual survival of large-bodied birds is low following severe winter dry seasons, and that small-bodied survivors migrate shorter distances to breeding areas, based on stable-hydrogen isotopes in feathers molted following reproduction (Studds & Marra, in prep). Because dry season rainfall in Jamaica also is becoming increasingly variable, such pressures could lead to annually shifting adaptive peaks for body size rather than to sustained directional selection (Grant and Grant 1989). How changing climate during the nonbreeding period might act on other targets of selection that could influence migration merits further study.

Further insights into the numerous potential responses migratory birds could display to changing climate during the nonbreeding season will require additional observational studies coupled with experiments. At present, the role of food as a limiting factor for nonbreeding season migratory birds in the Caribbean is known for

only a handful of species. Food supplementation experiments with Ovenbirds (*Seiurus aurocapilla*) (Brown and Sherry 2006) and individual upgrade experiments with redstarts (Studds and Marra 2005) clearly isolate the role of food and moisture as key limiting factors for birds during the late-winter dry season. Needed are long-term observational data and similar experimental approaches for Palearctic migrants while on their African and Asian nonbreeding grounds. Also needed are common garden and captive breeding experiments designed to clarify the relative role of genetic versus environmental controls on spring departure schedules. The latter will be particularly important for understanding how phenotypic plasticity and microevolutionary change could interact to shape spring migration schedules under changing environmental conditions (Pulido 2007).

Despite recent progress, our understanding of how climate during the nonbreeding season acts to affect individual condition, demography, and abundance of migratory passerines remains poor. Additional research during the nonbreeding period will help to develop a more synthetic view of how ongoing changes in climate in different phases of the annual cycle interact to influence year-round population processes in long-distance migratory birds. Such knowledge is critical to our understanding of population regulation (Sæther et al. 2004), to the development of models that predict population dynamics of migratory birds (Dolman and Sutherland 1995, Runge and Marra 2005), and to population management (Almaraz and Amat 2004).

Figure 5. Hypothesized influence of nonbreeding season rainfall on the performance

of American redstarts throughout their annual cycle. Solid arrows depict pathways

examined in this study, and dashed arrows show other potential effects.
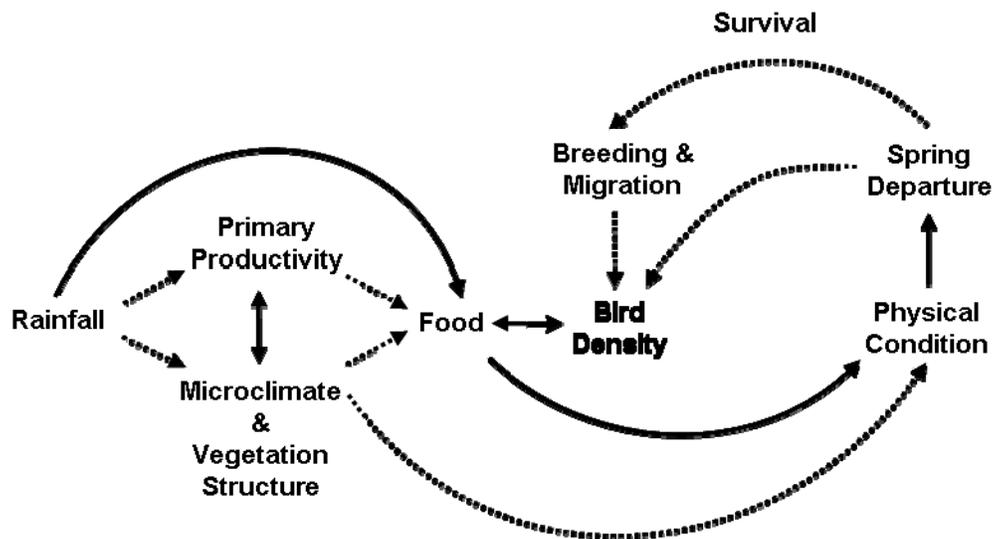
Figure 6. Trends in dry season rainfall (January–March) from 1995–2005 at the
Burnt Savannah climate monitoring station in Jamaica West Indies, approximately 10
km northwest of the nonbreeding site where redstarts in this study were monitored.
Insets show the monthly distribution of dry season rainfall during this study from
2002–2005. Data were provided by the Jamaica Meteorological Service.
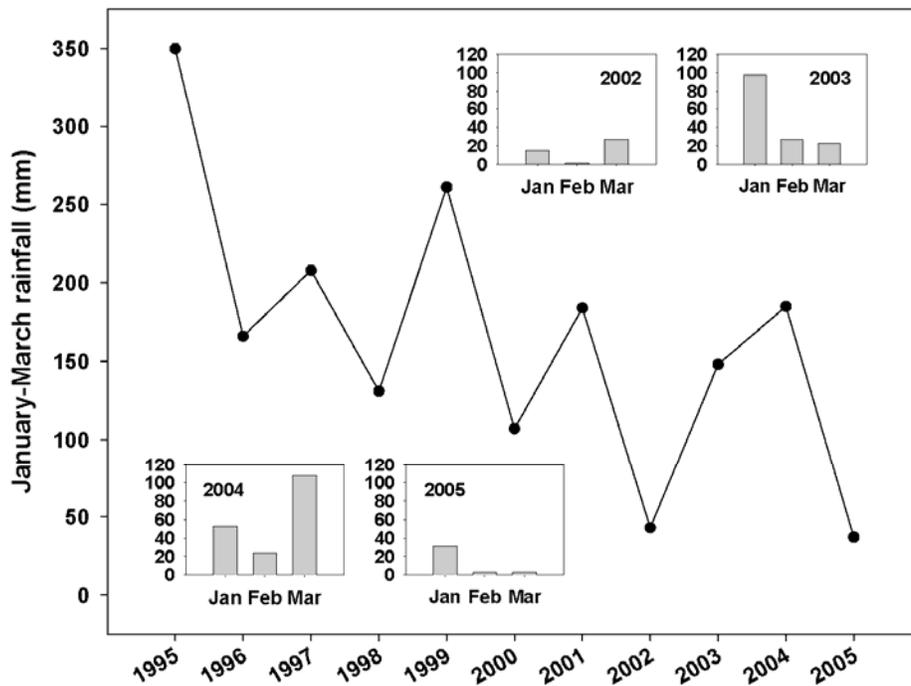
Figure 7. Relationship between dry season rainfall (January–March) from 2002–2005 and arthropod biomass (mean ± 1 SE) on the territories of American redstarts in mangrove forest (open circles) and second-growth scrub (filled circles) at a nonbreeding site in Jamaica, West Indies. Sample sizes are shown by numbers in parentheses.
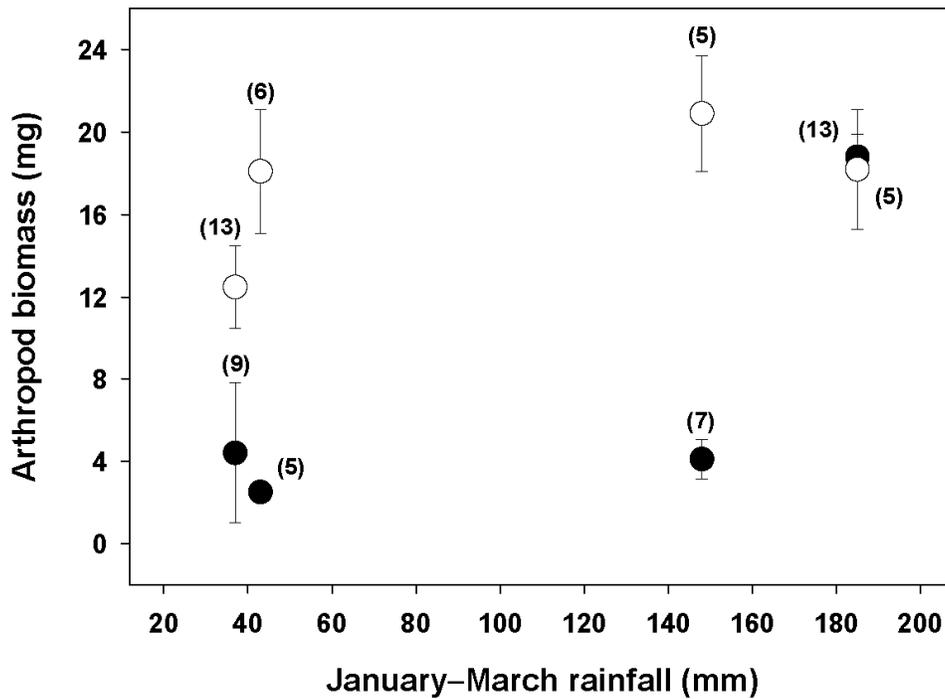
Figure 8. Relationship between dry season rainfall (January–March) from 2002–2005 and the corrected body mass (mass adjusted for wing chord, tail length, and tarsus size; mean ± 1 SE) of American redstarts overwintering in mangrove forest (open circles) and second-growth scrub (filled circles) at a nonbreeding site in Jamaica, West Indies. Sample sizes are shown by numbers in parentheses.
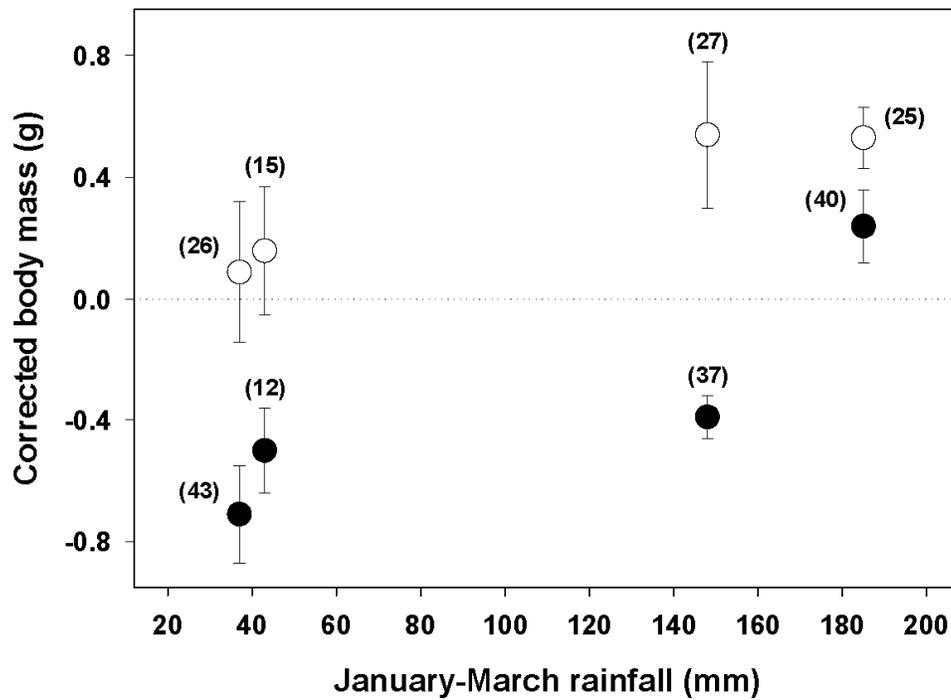
Figure 9. The relationship between the corrected body mass (mass adjusted for wing chord, tail length, and tarsus size) of American redstarts in mangrove forest (open circles) and second-growth scrub (filled circles) and their timing of departure on spring migration in each year from 2003-2005 at a nonbreeding site in Jamaica, West Indies.
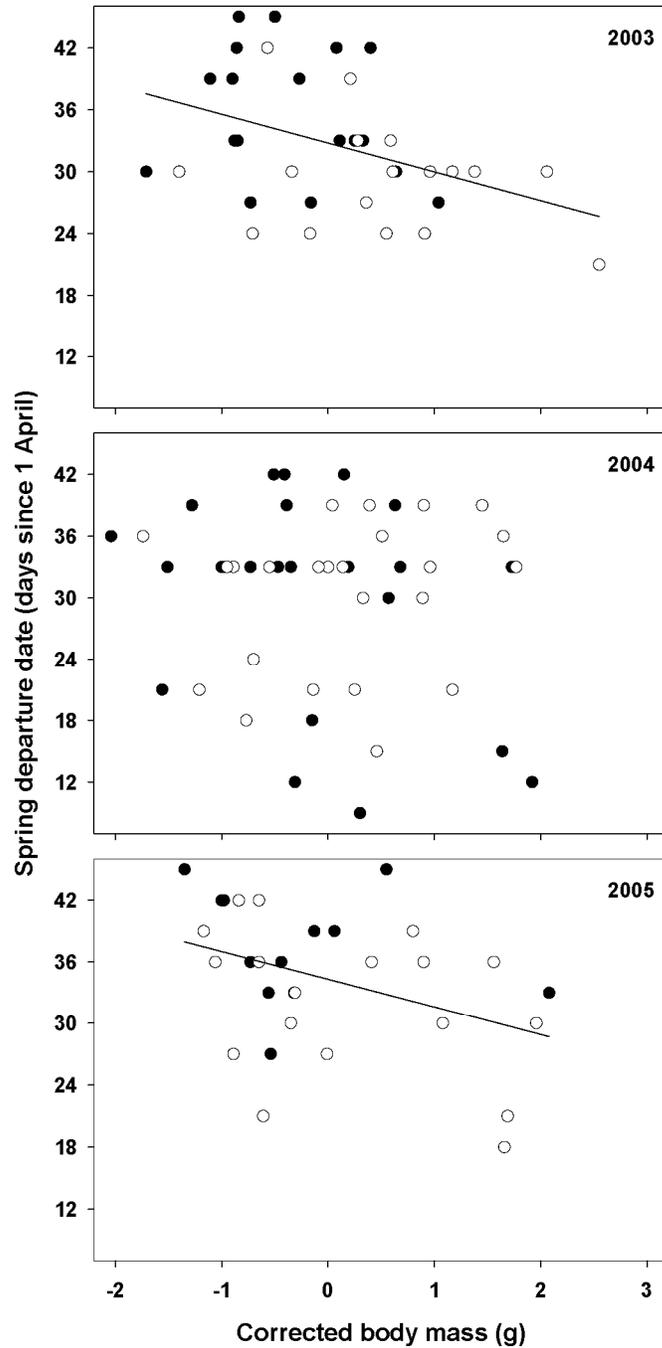
Figure 10. The relationship between corrected body (mass adjusted for wing chord, tail length, and tarsus size; mean ± 1 SE) and the timing of departure on spring migration (mean ± 1 SE) averaged across the years 2003-2005 for all American redstarts in mangrove forest (open circles) and second-growth scrub (filled circles).
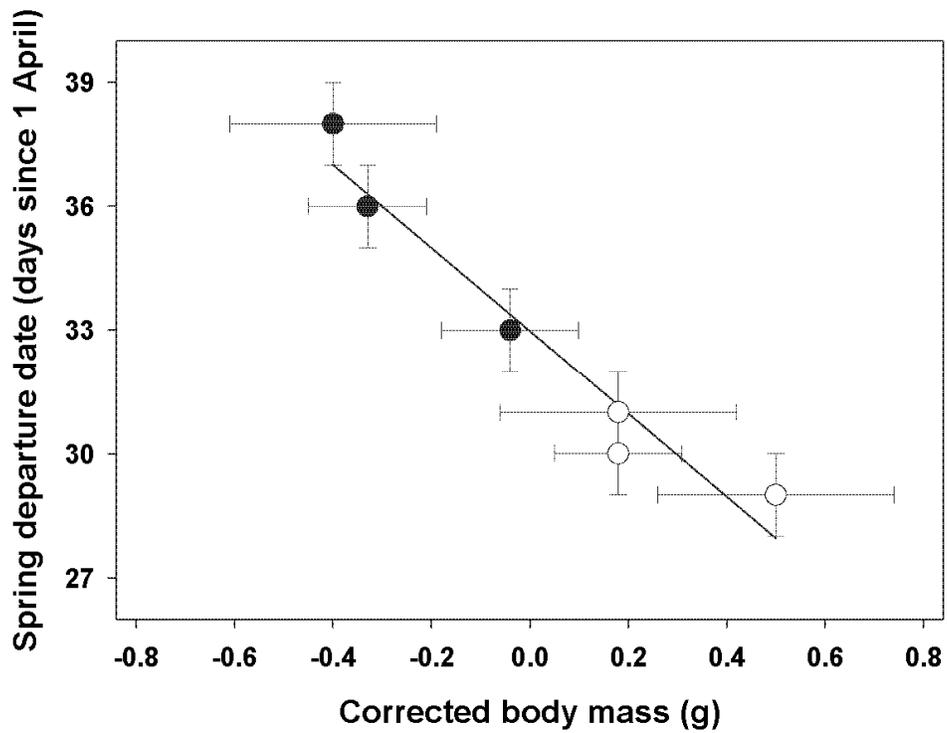
Chapter 3: Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird[3]

Abstract.   Natal dispersal, the process through which immature individuals permanently depart their natal area in search of new sites, is integral to the ecology and evolution of animals. Insights about the underlying causes of natal dispersal arise mainly from research on species whose short dispersal distances or restricted distributions make them relatively easy to track. However, for small migratory animals, the causes of natal dispersal remain poorly understood because individuals are nearly impossible to track using conventional mark-recapture approaches. Using stable-hydrogen isotope ratios in feathers of American redstarts (*Setophaga ruticilla*) captured as immature birds and again as adults, we show that habitat use during the first tropical nonbreeding season appears to interact with latitudinal gradients in spring phenology on the temperate breeding grounds to influence the distance traveled on the initial spring migration and the direction of natal dispersal. In contrast, adult redstarts showed considerable site fidelity between breeding seasons, indicating that environmental conditions did not affect dispersal patterns after the first breeding attempt. Our findings suggest that habitat occupancy during the first nonbreeding season helps determine the latitude at which this species of Neotropical-Nearctic migratory bird breeds throughout its life and emphasize the need to understand how events throughout the annual cycle interact to shape fundamental biological processes.

Introduction

Dispersal shapes the ecology and evolution of animals by regulating gene flow, linking subdivided populations, and influencing the distribution of species. In most animals, adult dispersal distances between breeding seasons are relatively short (Gaines and McClenaghan 1980, Berven and Grudzien 1990, Paradis et al. 1998), suggesting that these critical biological processes are driven mainly by natal dispersal, the process through which immature individuals permanently depart their natal area in search of their first breeding site. Accurately measuring natal dispersal has been notoriously difficult because juvenile survival rates are low compared to those of adults and dispersal distances often exceed study area boundaries (Koenig et al. 1996, Anders et al. 1997, Clobert et al. 2001). Research on natal dispersal has therefore focused on species that are relatively easy to follow due to their short dispersal distances or restricted distributions (Clobert et al. 2001). Studies of natal dispersal in small, migratory animals are rare in comparison because individuals are nearly impossible to track using conventional mark-recapture approaches. For all but a handful of these species, we are presently unable to measure natal dispersal, study its underlying causes, and develop appropriate conservation plans (Hansson et al. 2003, Winkler et al. 2005, Møller et al. 2006, Tittler et al. 2006).

Natal dispersal strategies are thought to arise from a complex interplay between genetic and environmental forces. In many organisms, the traits that determine natal dispersal potential have a genetic basis (Roff and Fairbairn 2001, Hansson et al. 2003, Pasinelli et al. 2004). However, expression of these traits and their ultimate role in directing natal dispersal patterns can depend on environmental

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conditions experienced by juveniles within the natal area or soon after they leave (Hansson et al. 2003, Pasinelli et al. 2004). In birds, evidence is accumulating that juveniles gather public information (PI) during the post-fledging period to assess the suitability of future breeding sites (Doligez et al. 2002, Nocera et al. 2006, Hénaux et al. 2007). Exploiting PI to enhance reproductive success requires that juveniles arrive on the breeding grounds sufficiently early to acquire high quality territories. Temperate zone residents and short-distance migrants may solve this problem by wintering as close as possible to future breeding areas, thereby enabling early arrival at preferred breeding sites (Cristol et al. 1999). In contrast, long-distance migratory birds spend the nonbreeding period in tropical habitats thousands of miles away from temperate breeding areas. The quality of nonbreeding habitat is known to influence overwinter body condition, the timing of departure on spring migration, and the date of arrival on temperate breeding grounds (Marra et al. 1998, Saino et al. 2004, Studds and Marra 2005). This inability to regulate breeding ground arrival time may prevent reliance on PI from the previous summer, and force immature birds making their first breeding attempt to use other settlement cues. We tested the hypothesis that habitat-specific differences in overwinter performance combine with latitudinal gradients in spring phenology on the temperate breeding grounds to influence natal dispersal patterns in one species of Neotropical-Nearctic migratory bird, the American redstart (*Setophaga ruticilla*).

From 2002-2006, we monitored the overwinter performance of redstarts in two habitats at a nonbreeding site in Jamaica: a wet, mangrove forest where food is abundant through the winter and a dry, second-growth scrub habitat where food

becomes scarce in late winter. We then estimated patterns of natal dispersal using stable-hydrogen isotope ratios (δD) in redstart tail feathers collected across multiple years. In North America, δD in growing season precipitation varies with latitude (IAEA 1994), and birds incorporate these signatures into their feathers via the supporting food web (Hobson and Wassenaar 1997). Because immature redstarts grow their feathers in the nest and adults molt their wing and tail feathers in late summer on or close to the breeding site (Pyle 1997, Langin et al. 2007), feathers collected on tropical nonbreeding areas allow inferences about natal or molting sites from the previous summer. We collected one tail feather from immature redstarts during their first nonbreeding season to estimate the latitude of the natal area, and a second feather one year later from the same individuals, if they returned as adults, to estimate the latitude of the first breeding attempt. We also sampled feathers from the same adult redstarts in each of two consecutive years to understand whether winter habitat occupancy influenced patterns of dispersal between breeding seasons. These multi-year δD profiles for the same individuals enabled us to examine the geography of dispersal without tracking banded birds throughout their annual cycle.

Methods

Fieldwork was conducted in southwestern Jamaica at the Font Hill Nature Preserve (18°02'N, 77°57'). In winter (15 Jan–20 Feb) of 2002–2005, we captured redstarts in mist nets, color-banded and processed them, and plucked a single tail feather for δD analysis. From 20 Mar–15 April of each year, we recaptured birds to assess overwinter change in body mass. We estimated the date of departure on spring migration by searching territories of color banded redstarts every 3 days from 1

April–15 May. When we failed to resight a bird, we rechecked the territory twice

more during the 3-day period and once more in the next 3-day period. On this final

visit, we broadcast a recording of redstart songs and chips for five bouts of 20

seconds interspersed with 30 seconds of silence. We considered birds to have left on

migration when the playback drew no response. In each winter following, we

captured color-banded redstarts returning from the previous winter in order to sample

a second feather for δD analysis.

Isotope analyses were done at the Queen's University Facility for Isotope

Research (QFIR). Feathers were washed of surface oils and debris in a 2:1

chlorform:methanol solution and air-dried under a fume hood for 48 hours. After

transport to QFIR, feathers were allowed to equilibrate with the local atmosphere for

72 hours. A small sample of each feather (0.10–0.15 mg) was clipped, loaded into a

silver capsule, and placed in a drying oven at 100°C for 24 hours to remove potential

surface water. The capsules were crushed, combusted at 1450°C in an elemental

analyzer (Finnegan TC/EA), and introduced online to an isotope ratio mass

spectrometer (Finnegan MAT Delta Plus XL). One in-house standard was run for

every five unknowns. We report isotope ratios in delta notation relative to Vienna

Standard Mean Ocean Water (VSMOW), where δD = (^{2}H/^{1}H$_{sample}$ / ^{2}H/^{1}H$_{standard}$)-1) $\times$

1000. Analytical error ($\pm$ 1 SD) was 2 ‰ based on replicate analyses of the same

feather (n = 18) and analyses of standards (kaolinite n = 11; brucite n = 12). We

adjusted the isotope ratio of each feather by +19 ‰ to account for isotopic

fractionation among precipitation, redstart prey, and feathers (Hobson et al. 2004).

The δD values reported here include both exchangeable and non-exchangeable

hydrogen. To minimize any potential systematic error caused by non-exchangeable hydrogen, we analyzed all feather samples during a period of six days and included a roughly equal number of feathers from each habitat and age-class in each run of the mass spectrometer.

We examined the relationship between spring departure schedules of immature redstarts and date of lilac bud burst at the latitude of their first breeding attempt using data from World Data Center of Paleoclimatology (WDCP) and a previously published δD base map (Dunn et al. 2006). We first assigned the δD ratio of each feather sampled after the first breeding attempt to one 10-‰ division on the δD base map. We then determined the average lilac bud burst date within each 10-‰ division of the δD base map. By assuming that the rate of migration was the same for individuals, we were able to assess whether immature redstarts used plant phenology as a cue for settling their first breeding territory.

We judged whether redstarts dispersed from or were faithful to their latitude of origin during the previous summer by calculating the 95 % confidence interval of δD in feathers sampled from separate population of redstarts ($\pm$ 9 ‰ , $n = 42$) known to have bred at the Queens University Biological Station, Ontario, Canada (44^o43', 76^o19') (Langin et al. 2007). In the present study, only individuals whose feathers from successive years had differences in δD in excess of $\pm$ 9 ‰ were considered to be dispersers. This cutoff likely caused us to label as site faithful some birds that actually dispersed short distances from their origin the previous summer. Despite the potential for such error, we believe this approach to defining dispersal events was

warranted given published estimates of variation in δD in feathers molted at the same latitude (Wunder et al. 2005, Rocque et al. 2006, Langin et al. 2007)

Data on overwinter body mass change were examined using a repeated-measures mixed model with year, sex, and habitat as main effects and season (winter and spring) as the repeated-measure. Data on natal and breeding dispersal were examined using a repeated-measures mixed model with year, sex, and habitat as main effects and bird age (immature and adult) as the repeated-measure. Tarsus length was included in each model as a covariate to adjust for body size differences. Individual bird nested within habitat was considered a random effect in each of the above analyses. Departure schedules were analyzed with a Kaplan-Meier log-rank test. The relationship between overwinter body mass change and migratory departure date, between migratory departure date and δD, and between migratory departure date and lilac bud burst date were tested using Pearson's correlation. Differences between the latitude of the first breeding attempt for birds wintering in mangrove and scrub were examined with Student's t-test. Comparisons between rates of natal and breeding dispersal were made with Pearson's chi-square test. All data met test assumptions, so no transformations were used. Analyses were done with SAS 8.2 (SAS Institute 1999).

Results

Regardless of sex or body size, immature redstarts wintering in mangrove forest maintained body mass over winter, whereas those in second-growth scrub lost mass (repeated measures mixed model for sex × season: $F_{1, 37} = 2.45$, $P = 0.13$; for body size: $F_{1, 37} = 1.05$, $P = 0.31$; for habitat × season: $F_{1, 37} = 5.52$, $P = 0.02$; +0.01 ±

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0.08 g for mangrove; -0.18 ± 0.07 g for scrub; mean ± 1 SE). Individuals that maintained mass departed earlier on spring migration than those that lost mass ($r = 0.48$, $P = 0.01$, $n = 27$), allowing redstarts in mangrove to leave an average of seven days ahead of those in scrub (Kaplan-Meier log rank test for habitat: $\chi^2 = 22.26$, $P < 0.0001$, $n = 78$; 31 ± 1 days since 1 April for mangrove; 38 ± 1 days since 1 April for scrub; mean ± 1 SE).

Of the 41 redstarts first captured during their first winter, 22 were recaptured the next year when they returned as adults. Feathers of recaptured birds indicated the date of departure on the first spring migration was positively correlated with the δD of the first breeding attempt ($r = 0.60$, $P = 0.004$, $n = 22$; Fig. 11A), but not with the δD of natal origin ($r = 0.09$, $P = 0.69$, $n = 22$; Fig. 12). Immature redstarts departing early from mangrove migrated comparatively short distances and made their first breeding attempt in the southern part of the breeding range, whereas later departing individuals from scrub migrated and made their first breeding attempt further north ($t_{20} = -2.88$, $P = 0.009$; Fig. 11B). Natal feathers of immature redstarts overwintering in mangrove forest and second-growth scrub had a similar range of δD values ($t_{20} = -0.34$, $P = 0.73$; Fig. 12), suggesting that the natal origin of each bird had little effect on the location of the first breeding attempt.

Breeding ground settlement patterns of immature redstarts were consistent with latitudinal differences in the start of the growing season, as indexed by lilac bud burst dates modeled from daily temperature extremes (Schwartz and Caprio 2003) Early-departing redstarts settled at latitudes with comparatively early lilac bud burst dates, while later departing birds settled at latitudes with later bud burst dates ($r =$

0.52, $P = 0.01$, $n = 22$; Fig. 13). It is unlikely that birds use lilac phenology as a cue for selecting breeding territories, but lilac budburst occurs during redstart migration, and can be considered a surrogate for the onset of photosynthesis in other plant species (Schwartz 1998). The apparent interaction between habitat-specific differences in spring departure schedules and breeding ground phenology resulted in marked differences in natal dispersal direction: regardless of sex and body size, individuals wintering in scrub dispersed north of their natal area, whereas birds wintering in mangrove dispersed south of their natal area (repeated measures mixed model for sex: $F_{1, 19} = 0.21$, $P = 0.66$; for body size: $F_{1, 19} = 0.36$, $P = 0.55$; for year × habitat: $F_{1, 19} = 5.07$, $P = 0.02$; Fig. 14A).

Consistent with our results from immature redstarts, adults wintering in mangrove maintained body mass, whereas those in scrub habitat lost mass (repeated measures mixed model for habitat × season: $F_{1, 41} = 8.60$, $P = 0.0008$; 0.00 ± 0.08 for mangrove; -0.24 ± 0.07 g for scrub; mean ± 1 SE). Adult redstarts in mangrove also departed earlier on spring migration compared to those in scrub (Kaplan-Meier log rank test for habitat: $\chi^2 = 16.82$, $P < 0.0001$, $n = 137$; 30 days since 1 April ± 1 for mangrove; 34 days since 1 April ± 1 for scrub; mean ± 1 SE). Despite the comparable overwinter performance of adults and immature birds, adult dispersal between breeding seasons was not influenced by winter habitat occupancy (repeated measures mixed model for year × habitat: $F_{1, 21} = 0.05$, $P = 0.83$; Fig. 14B).

δD can vary significantly among feathers grown at the same latitude, leading to potential bias in the interpretation of dispersal patterns (Wunder et al. 2005, Langin et al. 2007). We therefore used the 95 % CI of δD in redstart feathers molted at a

known location (± 9 ‰, $n = 42$) to judge whether birds truly dispersed from their latitude of origin (Langin et al. 2007). Based on this cut-off, the rate of natal dispersal was greater than the rate of adult dispersal between breeding seasons ($\chi^2 = 5.81$, $P = 0.02$; 7/22 natal dispersers; 1/23 adult dispersers).

Discussion

Our results indicate that environmental conditions in locations thousands of miles apart can interact across periods of the annual cycle to influence the distance and direction of natal dispersal in American redstarts. Immature redstarts securing territories in mangrove forest maintained body mass over winter, allowing them to depart earlier from Jamaica than individuals wintering in scrub and to undertake a shorter spring migration. Because migratory birds appear to use phenological cues to select breeding habitat and synchronize reproduction with food availability for nestlings (Thomas et al. 2001), early migrants probably benefit by settling in southern parts of the breeding range where the early vegetation flush supports an early food supply. Conversely, immature birds holding territories in second-growth scrub lost mass, forcing them to depart later and complete a longer migration. Birds departing later would need to migrate further north to locate necessary resources for breeding, or risk costly mismatches between food availability and nestling nutritional demands (Thomas et al. 2001, Both et al. 2006a). Immature birds arriving late could also find southern breeding areas saturated with early arrivals, creating additional stimulus to migrate further north in search of breeding territories. Because redstarts from both nonbreeding habitats fledged from a similar range of natal latitudes, birds spending

their first winter in mangrove ultimately dispersed south of their natal area, while those in scrub dispersed north of their natal area.

It could be argued that variation in individual quality determined the overwinter performance and dispersal direction of immature redstarts, not habitat occupancy itself. In autumn, immature redstarts arrive in Jamaica prior to adults and establish winter territories randomly with respect to habitat (Marra 2000). Dominance status in redstarts is a function of both sex and body size, allowing adult males and large-bodied adult females to displace many immature birds from mangrove forest (Marra 2000, Marra and Holmes 2001). This raises the possibility that variation in sex- and size-based competitive ability among immature redstarts ultimately controls overwinter performance and, thus, natal dispersal patterns. However, such effects were not apparent in the present study because neither sex nor body size mediated the effect of habitat occupancy on overwinter performance and dispersal. Additionally, previous research in this system has demonstrated that, regardless of sex and body size, immature males and females experimentally upgraded from second-growth scrub to mangrove forest maintained mass and departed earlier on migration compared to control redstarts that remained in scrub for the duration of the nonbreeding period (Studds and Marra 2005). Together, these data support the idea that winter habitat occupancy is the most important driver of overwinter performance in redstarts and suggest it was the underlying factor responsible for the natal dispersal patterns observed in this study.

In many species, immature birds identify future breeding sites through post-fledging exploration or by gathering PI near their natal site (Nocera et al. 2006,

Hénaux et al. 2007). These behaviors can be advantageous because they enable birds undertaking their first breeding attempt to settle in familiar areas where they have some knowledge of expected reproductive success (Doligez et al. 2002). Our results do not preclude the possibility that immature redstarts prospected for and identified future breeding territories near their natal site before leaving on fall migration. Indeed, the similarity between the δD of the natal and first breeding attempt for many redstarts is consistent with natal site fidelity, particularly for birds leaving during the middle of the spring departure period, when departure schedules from each habitat overlapped (Fig. 14A, days 36 and 39). It is interesting to note that during this six-day time frame, immature redstarts departing from mangrove forest tended to disperse south of their natal area, whereas the majority of those from scrub habitat dispersed north, even when they left their nonbreeding territories on the same day. One explanation for this pattern is that, prior to migratory departure, immature redstarts holding mangrove territories were in superior body condition compared to those in scrub. Initiating migration in good condition could facilitate a more rapid migration and earlier arrival at southern breeding areas by reducing refueling time at stopover sites, an idea supported by both orientation experiments and recapture rates of birds during spring passage (Yong and Moore 1997, Sandberg et al. 2002). Thus, the interaction between winter habitat occupancy and breeding ground phenology may have influenced natal dispersal patterns for redstarts we classified as site faithful as well as those we labeled dispersers.

Once redstarts gain breeding season experience, dispersal appears to become decoupled from environmental conditions experienced during the nonbreeding period.

The overwinter performance of adults was similar to that of immature birds, however, unlike immature redstarts, the habitat-specific spring departure schedules of adults did not conclusively influence patterns of breeding dispersal. After accounting for the potential environmental variation in feather δD, adults showed considerable breeding site fidelity, with only 4% (1/23) of birds dispersing away from the latitude occupied in the previous breeding season. Adult redstarts may not have returned to the exact location of their first breeding attempt; it is possible that they dispersed short distances to new breeding sites. Unfortunately, δD does not provide the resolution needed to distinguish between these possibilities. Nonetheless, this result suggests that the environmental conditions during the first nonbreeding season that drive natal dispersal patterns also appear to influence the location at which birds breed in future years. Because adult redstarts show high fidelity to nonbreeding territories (Marra and Holmes 2001), repeated use of the same nonbreeding sites could help synchronize spring departure schedules with phenology on breeding areas. Importantly, mismatches between breeding ground arrival time and resource phenology could still occur if environmental conditions on nonbreeding areas vary among years (Studds and Marra 2007).

Unfortunately, environmental change on nonbreeding areas appears certain. Multiple independent models of climate change predict significant long-term drying trends in the Caribbean region (Neelin et al. 2006), the primary nonbreeding range of many species of migratory songbirds (Wunderle and Waide 1993). Because moisture directly affects nonbreeding season arthropod populations, declining rainfall in future years could severely limit food availability for birds, resulting in progressively

delayed migration schedules (Marra et al. 1998, Studds and Marra 2007). In North America, climate change scenarios predict further advances in spring resource phenology (Zhang et al. 2004), meaning suitable resources for both early and late arriving birds may lay progressively further north than in the past. Climate change within the Caribbean could therefore promote longer natal dispersal distances, resulting in northern range shifts and the eventual disappearance of more southern populations.

Finally, our results underscore the need to understand how events throughout the annual cycle of migratory species interact to shape fundamental biological processes. Although caution should be exercised in estimating linear distances from δD values, dispersal movements greater than our chosen 95% CI of ± 9 ‰ likely correspond to distances of more than 250 km. Our evidence for broad-scale demographic exchange in redstarts is consistent with low levels of phylogeographic structure demonstrated for other species of Neotropical-Nearctic migratory birds (Lovette et al. 2004). Nonbreeding season events therefore appear to help structure breeding populations of redstarts at regional rather than local scales, making it unlikely that birds are adapted to local conditions on North American breeding areas.

Figure 11. Spring departure dates of immature American redstarts and the δD of their first breeding attempt. (A) Immature redstarts wintering in mangrove forest (red circles) tended to depart early on spring migration and migrate comparatively short distances, whereas redstarts in second-growth scrub (blue circles) were more likely to depart later and migrate longer distances. (B) As a consequence, immature birds from mangrove made their first breeding attempt in southern areas and those from scrub bred at more nothern sites.
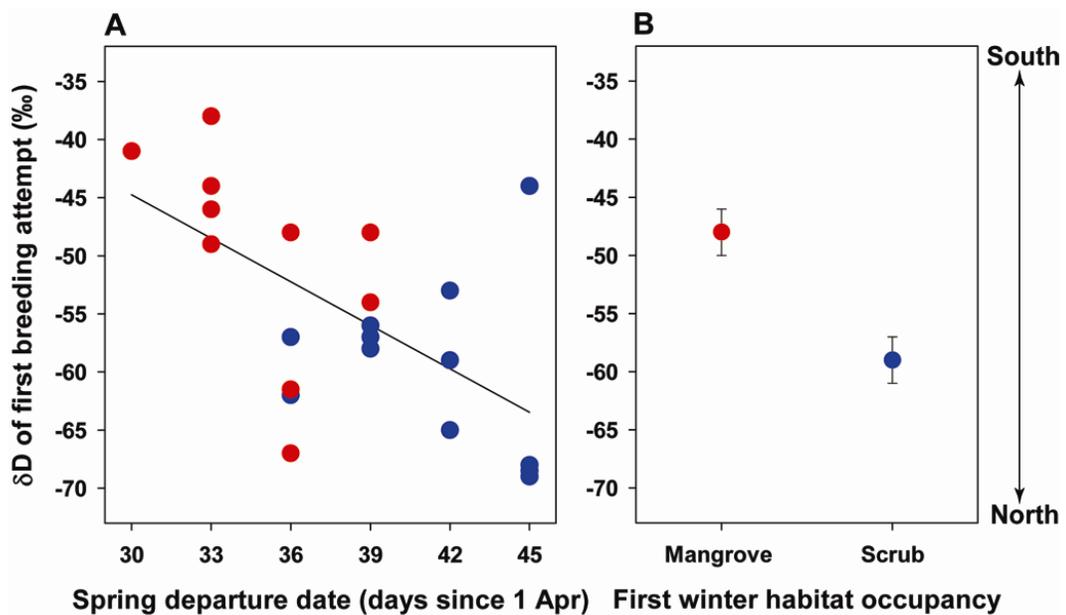
Figure 12. Spring departure dates of American redstarts and the δD of their natal

origin. Immature redstarts overwintering in mangrove forest (red circles) and second-

growth scrub (blue circles) did not differ in the δD of their natal origin, and there was

no conclusive relationship between the timing of departure from the nonbreeding

grounds and natal δD.
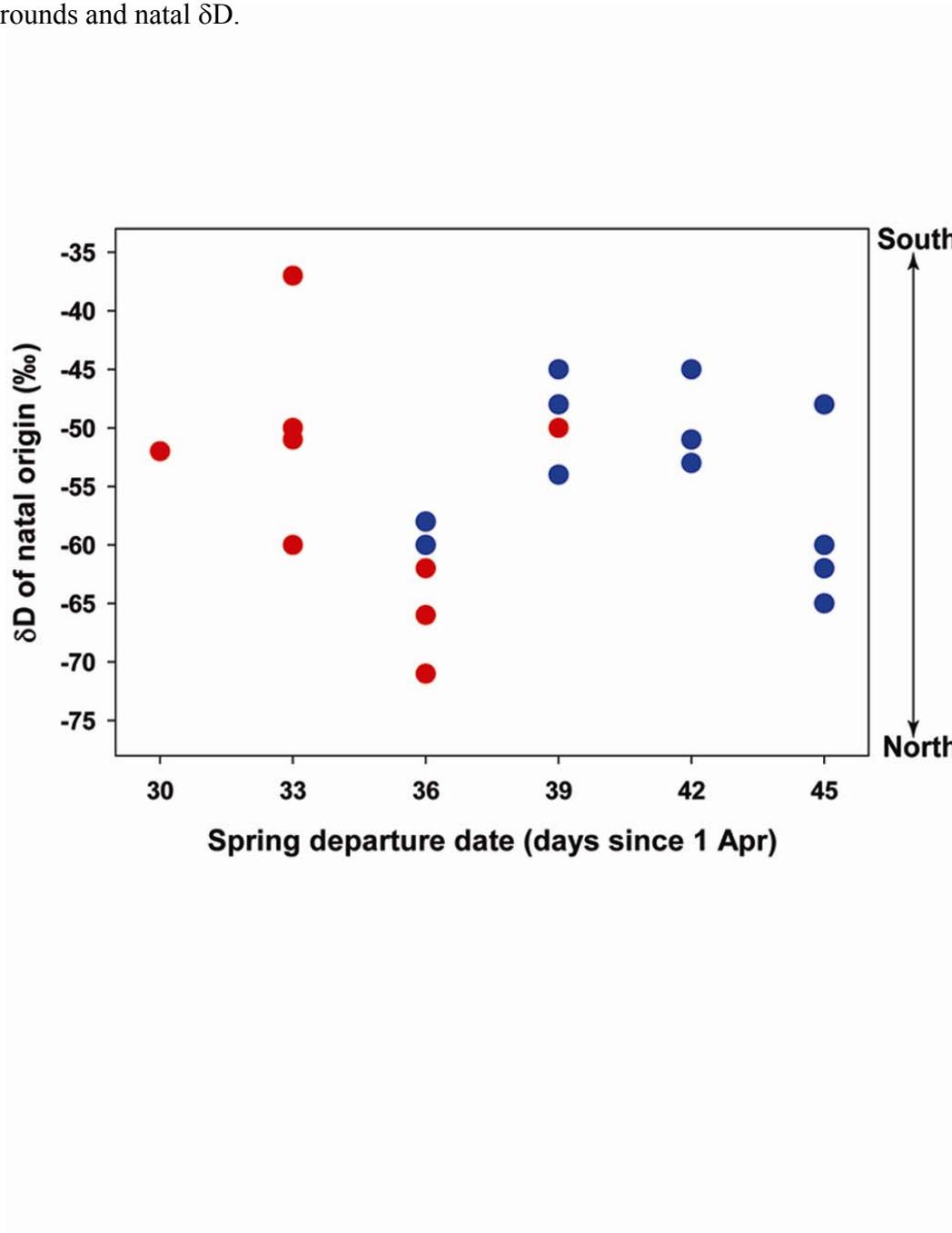
Figure 13. Spring departure dates of immature American redstarts and lilac bud burst dates at the δD of their first breeding attempt. Lilac bud burst dates index the start of the growing season at different latitudes, and are indicators of phenology in other plant species (Langin et al. 2007). The correlation between spring departure schedules of immature redstarts and lilac bud burst dates at the latitude of their first breeding attempt suggests that early-departing birds from mangrove (red circles) settled in southern breeding areas to exploit early plant phenology, while later-departing birds from second-growth scrub (blue circles) migrated further north to find suitable conditions.
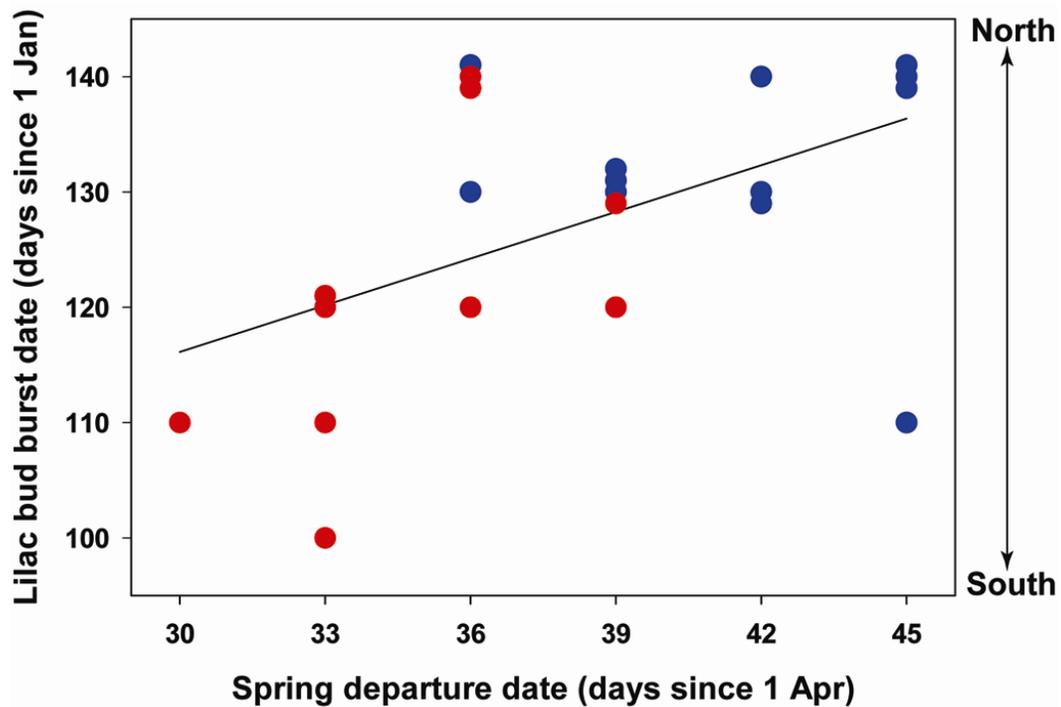
Figure 14. Dispersal patterns of American redstarts inferred from δD in tail feathers molted on or close to temperate breeding sites and sampled from the same individuals in consecutive nonbreeding seasons. (A) δD differences between adult and natal feathers (δD_{AF} - δD_{NF}) indicated that immature redstarts overwintering in mangrove and scrub habitats differed in their natal dispersal direction. Birds wintering in mangrove forest (red circles) dispersed south of their natal area, whereas redstarts in second-growth scrub (blue circles) dispersed north of their natal area. (B) δD differences between adult feathers in the second and first year of capture (δD_{AF2} - δD_{AF1}) showed that adult redstarts exhibited considerable breeding site fidelity, and that nonbreeding habitat occupancy had no apparent effect on adult dispersal. Horizontal dashed lines depict the 95% CI (± 9 ‰) of δD in feathers.
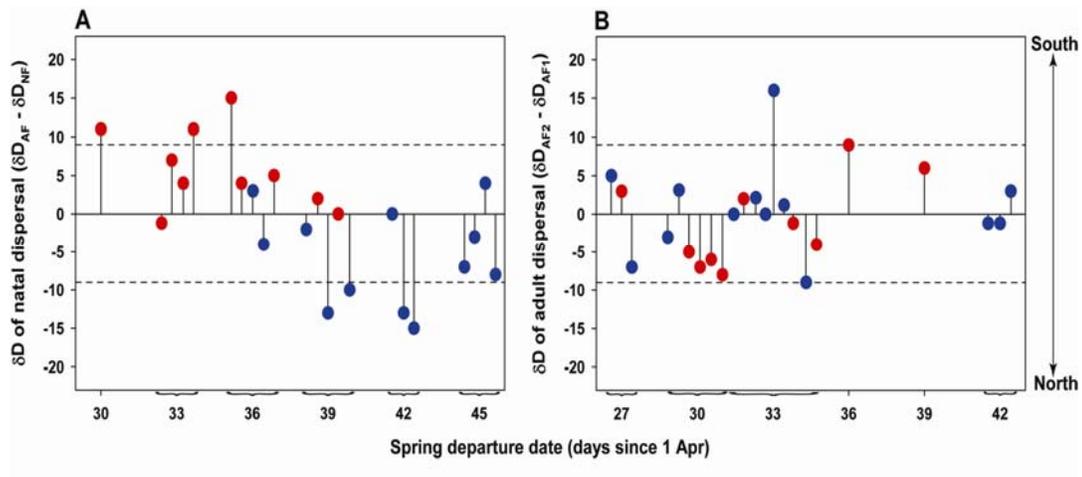
Chapter 4: Nonbreeding season selection on traits influencing survival in a migratory bird

Abstract.   Natural selection on traits that influence annual survival can be difficult to detect in migratory species because environmental conditions in one phase of the year may create pressures that do not exert mortality costs until another phase thousands of miles away. We evaluated phenotypic selection on three functionally related traits in a nonbreeding population of adult American redstarts (*Setophaga ruticilla*): body condition, the date of departure on spring migration, and breeding latitude as estimated through stable-hydrogen isotopes in tail feathers (δD). The form and strength of selection differed between black mangrove forest and second-growth scrub, two habitats that differ in their susceptibility to seasonal drought, and between two pairs of years that varied markedly in rainfall. Birds in both habitats experienced directional selection for short migration distance to southern parts of the breeding range, but this pattern was nearly twice as strong in dry, second-growth scrub compared to wet, mangrove forest. During winters where drought conditions prevailed, redstarts experienced stabilizing selection on spring departure dates and directional selection for short migration. In years of high rainfall, directional selection for shorter migration was comparatively weak and stabilizing selection on departure timing was not evident. These findings indicate that occupancy of drought-resilient habitat and years of high rainfall relax selection against migrating long distances and departing late. Information about spatial and temporal variation in

environmental conditions during the nonbreeding period is therefore needed to develop a more complete view of the selective pressures that influence the timing of migration and adaptation to changing climate.

Introduction

Although natural selection is a pervasive driver of evolutionary change, its magnitude varies among fitness components (Kingsolver et al. 2001). Across diverse taxa, both linear and quadratic forms of selection appear to be weaker for traits that affect survival than for those that influence reproduction (Hoekstra et al. 2001, Kingsolver and Pfennig 2007). However, survival selection may be stronger than is often appreciated because the environmental and temporal context in which it operates can make it difficult to observe. Unlike selection on reproductive traits, which can be studied annually, selection on traits that affect survival may occur only rarely with sufficient magnitude to be detected. Strong environmental perturbations, particularly those associated with weather or climate, may happen infrequently but can severely limit survival (Grant and Grant 1989, Brown and Brown 2000, Newton 2007), and studies that fail to encompass these episodes will likely underestimate the intensity of selection. Survival selection may also be hard to estimate because mortality is often not instantaneous, but is instead delayed until a later life-stage (Coulson et al. 2006, de Heij et al. 2006, Metcalf and Pavard 2007). These considerations make documenting survival selection especially challenging for migratory animals because these species inhabit geographically distant locations in different parts of the annual cycle, and environmental conditions in one phase can

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exert selective pressures that do not exact costs until another phase thousands of miles away (Marra et al. 1998, Sillett et al. 2000).

Long-distance migratory birds occupy numerous habitats as they move among temperate breeding areas, migratory stopover sites, and tropical nonbreeding quarters. Although selection pressures likely vary widely at these different locations, most estimates of annual survival come from the breeding grounds (McCleery et al. 1996, Cichon et al. 1998, Porneluzi and Faaborg 1999, Bayne and Hobson 2002, Dunn 2004). The relatively few studies conducted during the tropical nonbreeding season suggest that seasonal and annual variation in precipitation can also affect survival probability (Dugger et al. 2004). Annual survival between nonbreeding seasons is higher in winter habitats where edaphic conditions insulate plant and arthropod communities from seasonal drought (Marra and Holmes 2001, Johnson et al. 2006). In addition, survival between breeding seasons is often higher following winters of high rainfall (Szép 1995, Sillett et al. 2000, Dugger et al. 2004, Szép and Møller 2005, Saether et al. 2006). Despite the evidence for winter rainfall as a determinant of annual survival, we presently lack an understanding of which traits, if any, might be under selection. High levels of winter rainfall, as inferred from Normalized Difference Vegetation Index (NDVI) data, can also promote early arrival at breeding areas (Saino et al. 2004, Szép and Møller 2005, Pulido 2007, Saino et al. 2007). However, recent evidence suggests that declining rainfall in the tropics is impairing the ability of birds to migrate early (Neelin et al. 2006, Studds and Marra 2007), even as rising temperatures are intensifying selection for early arrival (Pulido 2007). Thus, an understanding of the traits under selection by nonbreeding season environmental

conditions is needed not only to refine our basic view of how selection acts on migratory birds throughout the annual cycle, but also to understand better the consequences of changing climate.

A fundamental obstacle to measuring survival in long-distance migratory birds is that most mortality occurs during the migratory period (Sillett and Holmes 2002). As a consequence, successfully measuring selection during the nonbreeding season requires integrating information about how environmental conditions carry over to cause mortality. Opportunistic and explicit measures of survival both during and at the conclusion of migration implicate inclement weather and predators as important sources of mortality (Moore et al. 1995, Brown and Brown 2000, Newton 2007). Individuals that must migrate longer distances may have a lower probability of survival because they are exposed to these hazards for longer time periods (Greenberg 1980, Nichols and Johnson 1990, Hestbeck et al. 1992).

Until recently, estimating migration distance was impossible for small songbirds because they are too small to carry transmitters of sufficient power, and the probability of following banded individuals throughout the year is extremely low. However, stable-hydrogen isotopes (δD), which vary with latitude as a function of continental-scale gradients in evapotranspiration, provide a promising solution to this problem. These isotopes are transferred up the food web and are incorporated into feathers that birds molt once each year on or close to temperate breeding sites (Hobson and Wassenaar 1997, Pyle 1997). Feathers sampled during the nonbreeding season therefore provide a chemical fingerprint of the approximate latitude at which birds bred the previous summer and thus permit an estimate of migration distance.

We tested the hypothesis that environmental conditions linked to rainfall during the nonbreeding season carry over to influence survival later in the year for a long-distance migratory bird, the American redstart (*Setophaga ruticilla*), by acting on three functionally related phenotypic traits: body condition, timing of spring migration, and breeding latitude as estimated using δD. American redstarts are highly territorial during the tropical nonbreeding period (Holmes et al. 1989, Marra et al. 1993). Adult males and large-bodied adult females preferentially occupy black mangrove forest, forcing smaller females and many juvenile males into adjacent, second-growth scrub habitat (Marra 2000). The availability of arthropods consumed as prey is typically two to three times greater in mangrove compared to scrub (Studds and Marra 2005, 2007), and birds in mangrove remain in good body condition at the conclusion of the nonbreeding period, whereas those in scrub decline in condition (Marra and Holmes 2001). Arthropod populations also fluctuate predictably with annual variation in rainfall, which enhances body condition in wet years and compromises condition during dry years for birds in both mangrove and scrub habitats (Studds and Marra 2007). Being in good condition at the conclusion of the nonbreeding period is advantageous because it enables timely departure on spring migration (Marra et al. 1998, Studds and Marra 2005), which, in turn, facilitates early arrival on breeding grounds (Marra et al. 1998) and greater reproductive success (Norris et al. 2004a, Reudink et al. in press)

Variation in spring departure schedules also plays an important role in determining the geographic distribution of redstarts on their breeding grounds. Multiyear δD feather profiles indicate that the date juveniles depart on their first

spring migration interacts with temperate zone phenology to influence the distance traveled to the first breeding site (Studds et al. 2008). Juveniles departing early from mangrove migrate to southern sites where spring phenology has advanced enough to provide adequate food, whereas those departing later from scrub migrate further to match the northward progression in phenology. Low between-year variation in δD of feathers from individual adults suggests that birds subsequently breed in the same geographic area throughout their life. Thus, redstarts wintering in scrub habitat must migrate longer distances each year to reach their breeding site compared to those in mangrove forest and may therefore face higher risk of mortality due to greater energetic cost, increased exposure to predators, or a higher probability of encountering severe weather conditions en route (Nichols and Johnson 1990, Hestbeck et al. 1992, Sillett and Holmes 2002, Newton 2007).

We compared the form and strength of selection between wet, mangrove forest and dry, second-growth scrub and between pairs of nonbreeding seasons that differed markedly in the amount of rainfall. We predicted that selection would be stronger for redstarts occupying scrub habitat because their poor body condition would force them to delay departure on migration and complete a longer journey to their intended breeding destination. We also predicted that dry years should lead to more intense selection than wet years because birds in both mangrove and scrub habitat would be in comparatively poor condition, requiring a later departure and a more rapid migration to reach their intended breeding site in sufficient time to breed. Because migration timing is also shaped by selection for early arrival at temperate

breeding areas, our analysis provided an opportunity to develop a more integrated view of migration schedules and how they may shift with changing climate

Methods

Study area

Fieldwork was conducted from 2002-2008 in southwestern Jamaica at the Font Hill Nature Preserve (18°02'N, 77°57') on twelve study plots that ranged in size from 1–5 ha. Six plots were dominated by black mangrove (*Avicennia germinans*), but had small patches of white (*Laguncularia racemosa*) and red mangrove (*Rhizophora mangle*). Mangrove stands typically had 0.5–1.0 m of standing water during January, but became drier in February and March, drying out entirely in some years. The other six plots were characterized by invasive second-growth thorn scrub. This habitat consists mainly of logwood trees (*Haematoxylon campechianum*), a thorny species with a fluted trunk, but also contained other less common species, including *Bursera simarubra*, *Terminalia latifolia*, and *Crescentia alata*. Unlike mangrove habitat, second-growth scrub rarely had standing water, and trees and other vegetation dropped most of their leaves during the dry season. All plots were gridded at 25-m intervals to aid the location of redstarts and mapping of their territories. Further description of the study area can be found in Marra and Holmes (2001).

Data collection

Throughout each spring (15 Mar–15 Apr), redstarts were captured in mist nets, aged and sexed using criteria from Pyle (1997), fitted with a unique color-scheme of plastic leg bands and USFWS aluminum bands, measured for body size, and weighed to the nearest 0.1 g. Body mass during this time reflects food

availability on the territory of each bird during the preceding month (Studds and Marra 2007), and is a good predictor of the date individuals leave their territories to initiate spring migration (Marra et al. 1998, Studds and Marra 2005). Prior to releasing birds, we also plucked a single tail feather that we later analyzed for its δD signature.

We delineated the territories of all color-banded redstarts that resided on study plots by following each bird for a minimum of three person-hours and recording its movements on gridded maps of study plots. We searched these territories every three days from 1 April–15 May to estimate the date redstarts left for spring migration. When we failed to resight a bird, we rechecked the territory twice more during the 3-day period and once more in the next 3-day period. On this final visit, we broadcast a recording of redstart songs and chips for five bouts of 20 seconds interspersed with 30 seconds of silence. We considered birds to have left their territories when the playback drew no response. Redstarts vary in their degree of aggressive response to audio playbacks (Marra 2000), but rarely fail to vocalize if they are present.

In each year following, we determined the apparent annual survival of color-banded birds by conducting intensive mist netting-efforts and visual searches of territories occupied during the previous year. Mark-recapture models suggest that mortality of long-distance migratory birds is extremely low during the stationary breeding and nonbreeding periods (Sillett and Holmes 2002). Thus, we assumed individuals that we failed to resight had died either on spring migration to the breeding grounds or on fall migration back to Jamaica.

We obtained rainfall data from the Jamaica Meteorological Service for the Burnt Savannah climate monitoring station, which lies approximately 10 km northwest of the study area. During 2003 and 2005, drought conditions prevailed, particularly during February and March (14 ± 13 mm rain; mean $\pm$ SD). In 2004 and 2007, rainfall in these months was markedly higher (98 ± 53 mm rain). We therefore classified these pairs of years as dry and wet, respectively.

Isotope analyses

We performed isotope analyses at the Queen's University Facility for Isotope Research (QFIR). Feathers were washed of surface oils and debris in a 2:1 chloroform:methanol solution and air-dried under a fume hood for 48 hours. After transport to QFIR, feathers were allowed to equilibrate with the local atmosphere for 72 hours. A small sample of each feather (0.10–0.15 mg) was clipped, loaded into a silver capsule, and placed in a drying oven at $100^{o}C$ for 24 hours to remove potential surface water. The capsules were crushed, combusted at $1450^{o}C$ in an elemental analyzer (Finnegan TC/EA), and introduced online to an isotope ratio mass spectrometer (Finnegan MAT Delta Plus XL). One in-house standard was run for every five unknowns. We report isotope ratios in delta notation relative to Vienna Standard Mean Ocean Water (VSMOW), where $\delta D = (^{2}H/^{1}H_{sample} / ^{2}H/^{1}H_{standard})-1) \times 1000$. Analytical error ($\pm$ 1 SD) was 3 ‰ based on replicate analyses of the same feather ($n = 18$) and analyses of standards (brucite $n = 13$; kaolinite $n = 16$). We adjusted the δD of each feather by +19 ‰ to account for isotopic discrimination among precipitation, redstart prey, and feathers (Hobson et al. 2004).

The δD values reported here include both exchangeable and non-exchangeable hydrogen. Feathers can exchange up to 25% of their unbound hydrogen with atmospheric moisture, causing δD to reflect partially the latitude of analysis (Wassenaar and Hobson 2000). One approach to controlling for this bias is to expose feathers to air with a known water vapor content prior to analysis, thereby standardizing the fraction of exchangeable hydrogen among samples (Wassenaar and Hobson 2000). However, internal laboratory results at QFIR indicate that drying feathers to remove surface water immediately before analysis, as was done in the present study, is equally effective at reducing error associated with exchangeable hydrogen. We analyzed all feather samples during a period of six days in 2006 and three days in 2007 and included a roughly equal number of feathers from each habitat and year in each run of the mass spectrometer.

Selection analyses

We restricted our analyses to adult redstarts because δD in their feathers permits inference about the distance of migration to breeding sites. In immature birds δD reflects natal origin in the previous summer, which is not informative about the distance they will later travel on spring migration (Studds et al. 2008). A total of 129 adults had data for all three traits ($n = 65$ in mangrove; $n = 64$ in scrub; $n = 59$ in wet years; $n = 70$ in dry years; Table 1).

We estimated the apparent survival of individual redstarts from one year to the next as a binary event (survivors = 1, non-survivors = 0) and converted these data to relative survival by dividing each observation by the proportion of redstarts that survived to the next year. To compare selection between habitats, we calculated

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relative fitness and standardized each trait separately within each habitat. For

comparisons between pairs of years that differed in rainfall, we computed relative

fitness and standardized trait values separately within each pair of years. We

standardized spring departure date and δD to mean 0 and unit standard deviation. To

standardize body mass, we first performed a principal components analysis (PCA)

using three morphological variables: unflattened wing chord, tail length, and tarsus

length. We then regressed body mass on the standardized factor scores from the first

principal component and the Julian date of capture. We included capture date as a

variable to adjust for potential variation in redstart mass across the one-month capture

period. The residuals of this procedure thus represented the mass of each bird

adjusted for its body size and date of capture, which can be interpreted as an index of

body condition.

To estimate direct selection on each trait, we calculated linear selection

gradients (β) from a model that included all linear terms for each standardized trait

and nonlinear (γ_{ii}) selection gradients from a model that contained both linear and

quadratic terms for each trait. When a fitness measure is a continuous variable, linear

regression on standardized traits yields partial regression coefficients that are

equivalent to standardized selection gradients, which measure the type and strength of

selection acting on each trait while holding values of all other traits constant (Lande

and Arnold 1983). Because redstart survival was measured as a dichotomous

response, selection gradients were calculated by using generalized linear mixed

models (GLMM) with binomial error structure. Each bird was included in the models

as a random effect because some individuals were sampled in more than one year.

Regression coefficients from GLMM are the logarithm of the odds of surviving given a unit change in a trait, and are therefore not comparable to selection gradients. Thus, to permit comparison of our results with those of other studies, we transformed GLMM coefficients to their approximate selection gradients following Janzen and Stern (1998).

We used a sequential model-building approach to evaluate variation in form and strength of selection between habitats and among pairs of years that differed in rainfall. To assess variation in linear selection, we fit a model that contained either habitat or year as a fixed effect and all trait values as covariates. We then compared this model to one that included all of the above factors as well as all two-way fixed effect × trait interactions. We similarly tested for variation in the strength of nonlinear selection, except that we built the initial model with a fixed effect and all linear and quadratic terms and then compared it to one that also had all two-way fixed effect × quadratic interactions. Because each model was a nested subset of the other, we compared them by using likelihood ratio tests and assessed their significance as a chi-square distribution with degrees of freedom equal to the difference in the number of variables in each model. All analyses were done in SAS 9.1.3 (SAS Institute 2003)

In animals with putatively open populations, such as long-distance migratory birds, estimates of annual survival will be less than true survival because an unknown number of individuals that are recorded as dead will have instead emigrated permanently to new areas (Burnham and Overton 1979). Mark-recapture techniques can offer a more robust estimate of annual survival by adjusting for resight probability, which is the probability that an individual categorized as dead in one year

is resighted in future years. We elected not to use this approach because <1% of birds (3/313) were known to have been classified mistakenly as dead over the entire study. Thus, mark-recapture estimates of survival would produce nearly identical results to GLMM analyses.

Results

Variation in selection between habitats

Linear selection

Based on δD in tail feathers grown on breeding areas, we detected significant, positive directional selection on migration distance among redstarts overwintering in both mangrove forest ($\chi^2 = 5.89$ $P = 0.02$; Fig. 15A) and second-second growth scrub ($\chi^2 = 4.37$, $P = 0.04$; Fig. 15B). However, selection was nearly twice as strong for birds occupying scrub habitat than for those in mangrove (Table 2). Patterns of δD did not vary for adults captured across multiple years ($F_{3,48} = 0.21$, $P = 0.89$), suggesting that redstarts did not compensate by shifting their breeding latitude between years. Because δD is lower at higher latitudes, the positive slope of these selection gradients indicated that annual survival was higher for redstarts that migrated to southern parts of the breeding range and lower for birds that traveled further north. Selection on spring body condition and spring departure date was weak for birds in both mangrove ($\chi^2 = 0.00$ $P = 0.98$; $\chi^2 = 0.18$, $P = 0.67$, respectively) and scrub habitat ($\chi^2 = 0.19$, $P = 0.66$; $\chi^2 = 0.70$, $P = 0.40$, respectively; Table 2). Overall, patterns of linear selection did not differ between black mangrove forest and second-growth scrub ($\chi^2 = 1.86$, $P = 0.60$).

Nonlinear selection

We found no evidence for nonlinear selection acting on birds within mangrove forest (body condition: $\chi^2 = 0.00$, $P = 0.97$; departure date: $\chi^2 = 0.09$, $P = 0.77$; migration distance: $\chi^2 = 0.44$, $P = 0.51$) or on those second-growth scrub (body condition: $\chi^2 = 2.55$, $P = 0.11$; departure date: $\chi^2 = 0.12$, $P = 0.72$; migration distance: $\chi^2 = 0.18$, $P = 0.67$; Table 2). Accordingly, trends in nonlinear selection did not differ between mangrove and scrub habitats ($\chi^2 = 1.62$, $P = 0.66$).

Variation in selection among years

Linear selection

During the dry years of 2003 and 2005, we found significant directional selection for short migration distance ($\chi^2 = 6.51$, $P = 0.01$; Fig. 16A), but found no indication of selection on spring body condition ($\chi^2 = 0.04$, $P = 0.84$) or spring departure date ($\chi^2 = 0.44$, $P = 0.50$; Table 3). In the wet years of 2004 and 2007, directional selection for short migration distance only approached significance ($\chi^2 = 3.26$, $P = 0.07$; Fig. 16B), and neither spring body mass nor spring departure date were under selection ($\chi^2 = 0.29$, $P = 0.59$; $\chi^2 = 0.85$, $P = 0.36$, respectively; Table 3). Despite differences in the strength of selection on migration distance, we detected no overall difference in linear selection between pairs of years that varied in rainfall ($\chi^2 = 1.78$, $P = 0.62$).

Nonlinear selection

We found a nearly significant difference in patterns of nonlinear selection between pairs of dry and wet years ($\chi^2_3 = 7.16$, $P = 0.07$), a result that likely was related to variation in the form of selection on departure date. In the dry years of

2003 and 2005, we detected significant, negative nonlinear selection on departure date ($\chi^2 = 4.22$, P = 0.04), a pattern consistent with stabilizing selection, but not on body condition ($\chi^2 = 0.39$, $P = 0.53$) or migration distance ($\chi^2 = 064$, $P = 0.42$; Table 3). In contrast, in the wet years of 2004 and 2007, we found no evidence for nonlinear selection on departure date ($\chi^2 = 3.45$, $P = 0.10$; Table 2) or on body condition ($\chi^2 = 0.50$, $P = 0.48$) and migration distance ($\chi^2 = 0.62$, $P = 0.43$)

Discussion

Our results demonstrate that the form and strength of phenotypic selection through annual survival are dependent on both spatial and temporal variation in moisture that American redstarts experience during their nonbreeding period. Using δD in tail feathers, we found directional selection on breeding latitude for redstarts holding territories in wet, mangrove forest and for those in dry, second-growth scrub, with birds migrating to the southern part of the breeding range experiencing higher annual survival than those that traveled further north. However, selection was nearly twice as strong for birds in scrub than for those in wet, mangrove forest, suggesting that occupying moist habitats offset the survival cost of completing a long migration. We detected qualitatively similar effects of moisture when we examined variation in selection between pairs of years that differed in nonbreeding season rainfall. During years with low rainfall, redstarts experienced both stabilizing selection on spring departure date and directional selection for shorter migration distance, irrespective of their body condition prior to spring migration. In contrast, in years of high rainfall, directional selection for short migration distance was comparatively weak and

stabilizing selection on departure timing was not apparent. Thus, access to moist

conditions appeared to relax selection against long migration distance and late

departure.

When considered in conjunction with previous research on the factors

governing natal dispersal, these data illustrate sufficient complexity in the processes

that interact between phases of the annual cycle and across life-stages to influence

annual survival of American redstarts. Through the combined effects of late

departure on their first spring migration and the northward advance in temperate zone

phenology, immature redstarts holding territories in second-growth scrub disperse to

breed further north compared to birds inhabiting mangrove forest during their first

winter (Studds et al. 2008). The low between-year variation in δD of adult feathers in

both this and in the present study implies substantial fidelity to the same breeding

area and demonstrates that birds do not respond to selection for minimizing migration

distance by shifting their breeding latitude further south between breeding seasons.

Because immature redstarts that return to Jamaica in later years also show strong

fidelity to nonbreeding territories (Marra and Holmes 2001), adults become fixed not

only in their migration distance but also in the selective pressures on breeding latitude

that vary between nonbreeding habitats as a function of seasonal and annual variation

in rainfall.

Difference in the strength of selection on migration distance experienced by

birds in mangrove and scrub is consistent with divergence in the availability of

arthropods consumed as prey that occurs between these habitats during the late winter

dry season. Seasonally declining rainfall in the tropics leads to differential reductions

in arthropod populations among habitats that vary in their resistance to drought (Janzen and Schoener 1968, Wolda 1978, Strong and Sherry 2000, Johnson and Sherry 2001). The tendency for mangrove habitats to retain standing water well into the dry season helps to support high prey availability, allowing redstarts to remain in good body condition during the time when they are preparing to undertake spring migration (Marra et al. 1998, Studds and Marra 2005, 2007). Conversely, the inability of scrub habitat to hold moisture induces plants to shed their leaves as the dry season progresses. As a consequence, food resources become progressively scarce (Parrish and Sherry 1994, Brown and Sherry 2006) and redstarts decline in body condition (Marra and Holmes 2001, Studds and Marra 2005). Thus, superior body condition of redstarts in mangrove habitat may have better prepared them better to survive the rigors of long distance migration. Given previous evidence for the functional importance of body condition in migratory preparation (Marra et al. 1998, Studds et al. 2008), it is somewhat surprising that we did not consistently detect selection on this trait. One explanation for this result is that we ceased sampling body condition at the onset of the migratory period. The time lag between this measurement and each bird's departure date could have led us to underestimate selection on this trait.

Differences in selection across years that varied in nonbreeding season rainfall provide additional evidence of precipitation as an important selective agent. The simultaneous occurrence of stabilizing selection on departure date and directional selection for shorter migration distance in years with low rainfall suggests that selective pressures differed at either end of the departure period. During the dry

winters of 2003 and 2005, extremely low food availability caused poor body condition in redstarts in both habitats (Studds and Marra 2007), a situation that may have limited the survival of even early departing birds that migrated to the southern part of the breeding range. Although poor body condition may have also compromised the survival of later departing birds, strong directional selection against longer migration can account for the high mortality of these individuals. It remains unclear how departure on migration during a narrow time window in the middle of the departure period permitted birds to maximize their survival in dry years.

Although our results implicate rainfall during the nonbreeding period as an important agent of selection on breeding latitude, they do not provide information about the timeframe within a year mortality is most likely to occur. Two non-exclusive scenarios could lead to the observed variation in survival across breeding latitudes. First, it is possible that variation in survival with breeding latitude reflects a cost of migration, as has been demonstrated in several species of waterfowl (Nichols and Johnson 1990, Hestbeck et al. 1992). This cost could be exacerbated if departing wintering or staging areas in poor body condition forces a slower a pace of migration and increases the probability of encountering severe weather or predators (Moore et al. 1995, Yong and Moore 1997, Sandberg et al. 2002, Newton 2007). A second possibility is that latitude-specific survival occurs as a cost of reproduction. Trade-offs between survival and reproduction are ubiquitous in animals (Stearns 1992, Roff 2002), and frequently occur as a function of latitude (Kokita 2003, Sears and Angilletta 2003, Ardia 2005). In redstarts, clutch size varies with latitude, with birds breeding in Alberta laying an average of one egg more per clutch compared to those

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in Louisiana (Sherry, in prep). Our finding that survival shows the opposite trend with latitude suggests the existence of latitudinal trade-off between survival and reproduction in redstarts, and raises the possibility that it could be mediated, at least in part, by ecological processes operating during the nonbreeding period of the annual cycle.

Our results also suggest that understanding how long-distance migratory birds are likely to adapt to climate change requires considering selective pressures that occur during all phases of the annual cycle. Climate warming is intensifying selection for early arrival on temperate breeding areas by advancing plant and arthropod phenology and constricting the availability of these resources into an increasingly narrow time window (Post et al. 2001, Visser and Holleman 2001). Despite substantial variation, most species are arriving earlier and initiating nests sooner than in past (Cotton 2003, Dunn 2004). Considerable debate has arisen about whether shifts in the timing of these events are due to microevolution or to phenotypic plasticity (Przybylo et al. 2000, Jonzén et al. 2006, Both 2007, Gienapp et al. 2007). Findings here suggest that data on breeding season events, by themselves, are not sufficient to distinguish between these processes. Heritability in the timing of migration has been demonstrated for some species (Berthold and Pulido 1994, Møller 2001, Pulido et al. 2001), suggesting that this trait could evolve in response to selection. However, research that uses only data for breeding ground arrival date to search for evidence for evolution in the timing of migration may overestimate the role of rising temperatures if rainfall during the nonbreeding season is a common agent of selection on traits that influence annual survival in other species. Moreover, the

apparent response to selection for early arrival could appear stronger at nothern parts

of the breeding range because birds may experience high mortality en route as a

function of the environmental conditions they encounter in winter. Similarly, plastic

adjustment of migration dates likely involves relationships among numerous

functionally related traits, with the actual timing of migration being only one

example. Redstarts that survived for the duration of the study successfully negotiated

fluctuating selective pressures on body condition, the timing of spring departure, and

migration distance. Thus, the behavioral and physiological mechanisms underlying

phenotypic plasticity are likely to be extremely complex, and unraveling them will

likely require new approaches for studying individual birds throughout the year.

Table 1. Sample sizes used for analysis of selection on body condition,

date of departure on spring migration, and migration distance (δD), three

phenotypic traits hypothesized to influence annual survival of American

redstarts in Jamaica, West Indies.

	2003, 2005 (dry)	2004, 2007 (wet)	Total
Black mangrove	33	32	65
Second-growth scrub	37	27	64
Total	70	59	129

Table 2. Selection gradients ± 1 SE for annual survival of American redstarts in Jamaica, West Indies calculated separately for black mangrove and second-growth scrub habitat. Coefficients in boldface were significant at $P < 0.05$.

	Habitat	
	Black mangrove	Second-growth scrub
Linear (β)		
Body condition	0.011±0.064	0.029±0.081
Departure date	−0.020±0.063	0.125±0.118
Migration distance (δD)	**0.133±0.067**	**0.257±0.111**
Quadratic (γ_{ii})		
Body condition	0.002±0.061	0.727±0.455
Departure date	−0.015±0.052	−0.129±0.366
Migration distance (δD)	0.040±0.060	0.056±0.130

Table 3. Selection gradients ± 1 SE for annual survival of American redstarts in Jamaica, West Indies calculated separately for pairs of years that varied in the amount of nonbreeding season rainfall. Coefficients in boldface were significant at $P < 0.05$.

	Year	
	2003, 2005 (dry)	2004, 2007 (wet)
Linear (β)		
Body condition	−0.013±0.066	0.047±0.087
Departure date	0.053±0.079	−0.068±0.073
Migration distance (δD)	**0.200±0.078**	0.154±0.085
Quadratic (γ_{ii})		
Body condition	0.036±0.507	0.076±0.107
Departure date	**−0.223±0.114**	0.159±0.100
Migration distance (δD)	0.087±0.109	0.058±0.073

Fig. 15. Standardized linear selection gradients demonstrating that selection on migration distance influences the annual survival of American redstarts in (A) mangrove forest ($n = 65$) and (B) second-growth scrub habitat ($n = 64$).
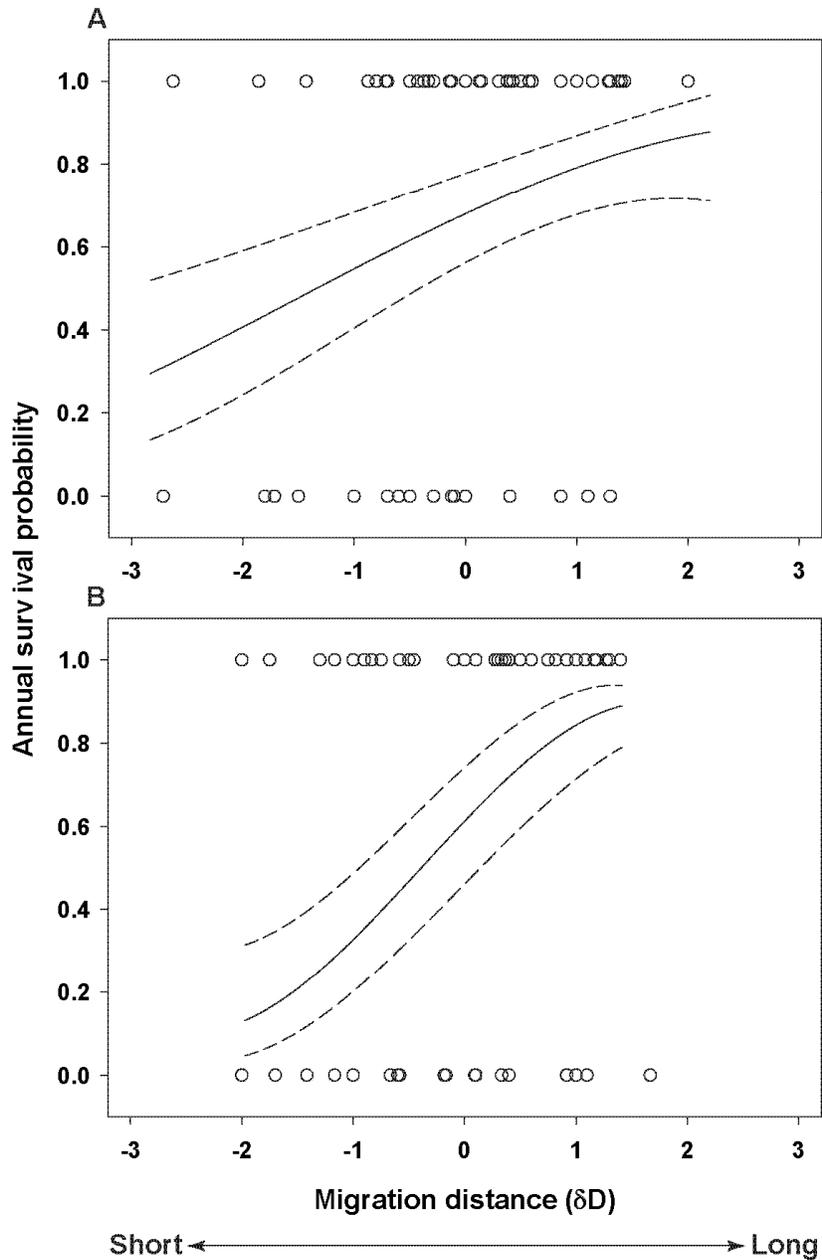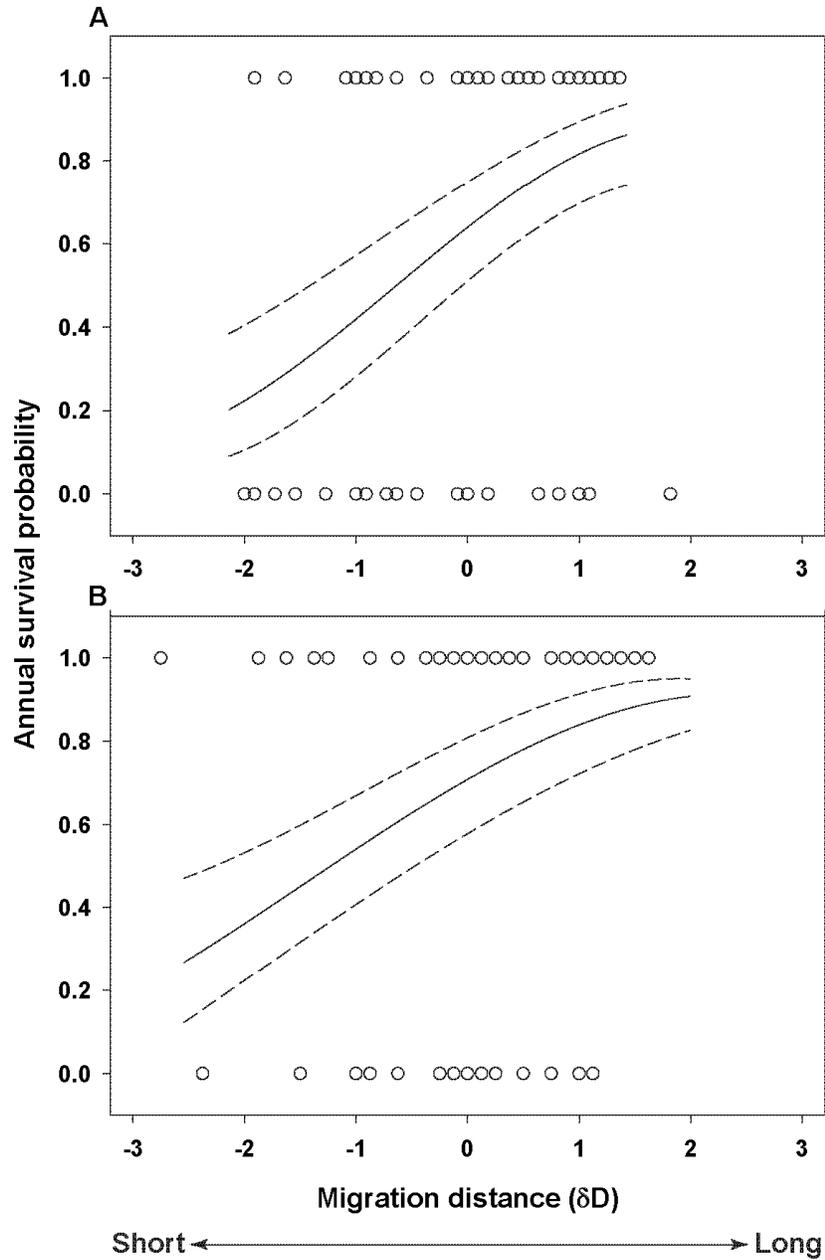
Fig. 16. Standardized linear selection gradients demonstrating that selection on migration distance influences the annual survival of American redstarts in nonbreeding seasons of (A) low rainfall ($n = 70$) and (B) high rainfall ($n = 59$).

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