



Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*

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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. However, conditions on tropical nonbreeding quarters 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 2 contrasting habitats: wet, mangrove forest and dry, second-growth scrub. From 2002 to 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 3 out of 4 yr, 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 tropical regions is projected to decline drastically over the next 50 yr, 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 response to rising temperatures at breeding areas.

KEY WORDS: American redstart · Climate change · Migratory birds · Seasonal interactions · *Setophaga ruticilla* · Spring migration

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1. INTRODUCTION

It is now clear that persistent shifts in climate are altering the structure and function of ecosystems worldwide (Walther et al. 2002, Parmesan & 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 rela-

tively 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 & Winkler 1999), and extended their ranges poleward (Thomas & Lennon 1999, Hitch & Leberg 2007). In other species, arrival times at breed-

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ing areas have remained unchanged as temperatures have increased (Mills 2005), or have not advanced enough to remain in synchrony with changes in resource phenology at lower trophic levels (Both & 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 & te Marvelde 2007, this issue). 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 & 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 have been shown to influence abundance, first arrival dates, and annual survival at breeding areas in Europe (Møller 1989, Kanyambwa et al. 1990, Peach et al. 1991, Szép 1995, Barbraud et al. 1999, Gordo et al. 2005). Indices of global climate cycles (e.g. El Niño Southern Oscillation, ENSO), which correlate well with temporal rainfall dynamics, have also been linked to the annual survival of migratory birds wintering in the Caribbean (Silllett 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 & Møller 2005), and the onset of breeding (Both et al. 2006).

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), insect abundance (Polis et al. 1997), and food plant quality for phytophagous insects (Huberty & 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 & 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, Wolda & Wright 1992, Lefebvre et al. 1994, Parrish & Sherry 1994). 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. 2004). 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 & 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 & 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 & Holberton 1998), lose mass over winter (Marra & Holmes 2001), depart later on spring migration (Marra et al. 1998, Studds & Marra 2005), and have lower annual survival (Johnson et al. 2006). Redstarts occupying dry winter habitats also arrive later at 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. 2004). 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. 1). 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.

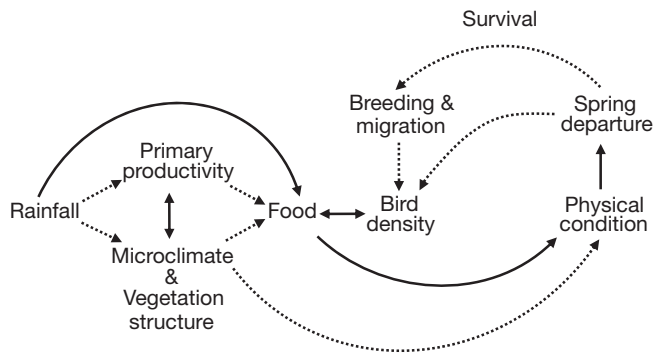


Fig. 1. *Setophaga ruticilla*. Hypothesized influence of non-breeding season rainfall on the performance of American redstarts throughout their annual cycle. Solid arrows: pathways examined in the present study; dashed arrows: other potential effects

2. MATERIALS AND 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 (<1000 mm of rain per year), and, as is typical of many tropical regions, experiences strong seasonality in precipitation. Rainfall is high from August through November, when average monthly rainfall typically exceeds 100 mm, and then usually declines to <25 mm mo^{-1} during the dry season from January through March (Jamaica Meteorological Service unpubl. data).

American redstarts were studied in 2 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 recemosa* 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 to 15 m, and had dense canopies averaging about 12 m in height. Mangrove stands were usually inundated with 0.5 to 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 to 8 cm dbh, grew from 3 to 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 & Holmes (2001).

In spring (15 March to 15 April) of 2002 to 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 3 h spread across at least 1 mo. From 1 April to 15 May of each year, we resighted color-banded birds at 3 d 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 d period, and then once again in the next 3 d 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 d interval of the spring departure period.

Arthropods available as redstart prey were measured in both habitats within 2 wk 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% ethanol, and later dried at 50°C for 24 h. All arthropods >2 mm in length that are typically found in regurgitation and fecal samples (Sherry & Holmes 1997) were then weighed (± 0.1 mg) to yield a single measure of food availability at each territory.

Trends in January through March rainfall from 1995 to 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 through March of each year as a linear covariate, and all 2-way interactions between demographic groups and environmental variables. We also included the day of the year of capture as a covariate in the analysis of corrected body mass to adjust for potential variation in redstart mass across the 1 mo 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).

3. RESULTS

From 1995 to 2005, dry-season rainfall (January through March) decreased by approximately 17% ($r = 0.64$, $n = 11$, $p = 0.03$; Fig. 2). 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. 2), 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.

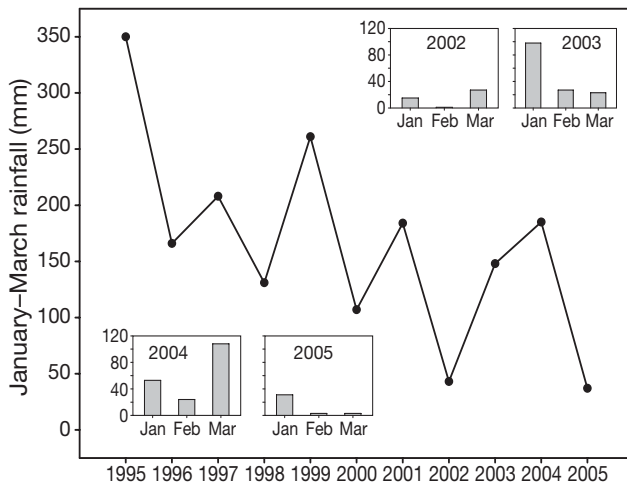


Fig. 2. Trends in dry-season rainfall (January through March) from 1995 to 2005 at the Burnt Savannah climate monitoring station in Jamaica, West Indies, approximately 10 km northwest of the nonbreeding site where American redstarts in this study were monitored. Insets show the monthly distributions of dry-season rainfall during this study from 2002 to 2005. Data were provided by the Jamaica Meteorological Service

During the dry seasons of 2002 to 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 \times Habitat: $F_{1,51} = 2.00$, $p = 0.16$; Fig. 3). 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. 3). The variation in food availability between habitats was pronounced in 3 out of 4 yr (2002: 20.9 ± 2.8 mg in mangrove, 2.6 ± 3.0 mg in scrub; means \pm SE; 2003: 18.1 ± 3.0 mg in mangrove, 4.1 ± 2.6 mg in scrub; 2005: 12.5 ± 1.9 mg in mangrove, 4.4 ± 2.4 mg in scrub). However, in the extremely wet spring of 2004 (Fig. 2), arthropod biomass in scrub was roughly equal to that in mangrove (18.2 ± 1.9 mg in mangrove, 18.8 ± 3.1 mg 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 \times Rainfall: $F_{1,51} = 0.00$, $p = 0.96$; for Age \times Habitat: $F_{1,51} = 1.74$, $p = 0.19$; for Sex: $F_{1,51} = 0.21$, $p = 0.65$; for Sex \times Rainfall: $F_{1,51} = 0.05$, $p = 0.82$; for Sex \times 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 \times Habitat: $F_{1,214} = 1.20$, $p = 0.27$; Fig. 4). Birds overwintering in mangrove forest had higher corrected mass compared to those in second-growth scrub in all 4 yr (GLM for Habitat: $F_{1,214} = 9.73$, $p = 0.002$; Fig. 4). 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 con-

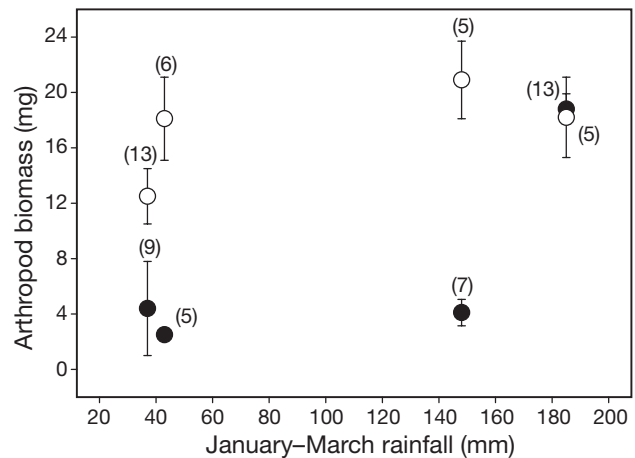


Fig. 3. Relationship between dry-season rainfall (January through March) from 2002 to 2005 and arthropod biomass (mean \pm SE) in the territories of American redstarts in mangrove forest (open circles) and second-growth scrub (filled circles) at a nonbreeding site in Jamaica, West Indies. Sample sizes are shown in parentheses

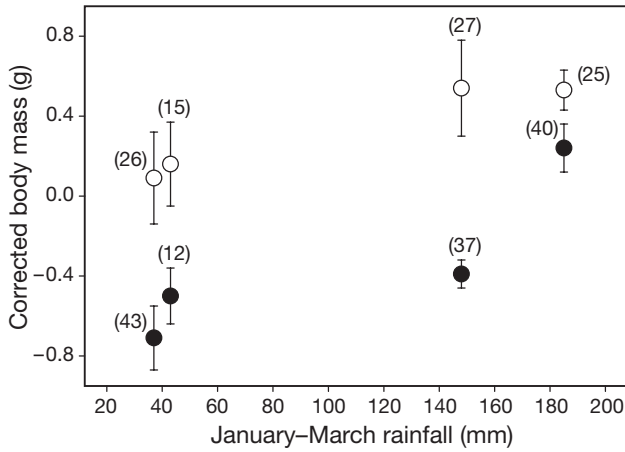


Fig. 4. *Setophaga ruticilla*. Relationship between dry-season rainfall (January through March) from 2002 to 2005 and the corrected body mass (mass adjusted for unflattened wing chord, tail length, and tarsus size; mean \pm SE) of American redstarts overwintering in mangrove forest (open circles) and second-growth scrub (filled circles) at a nonbreeding site in Jamaica, West Indies. Sample sizes are shown in parentheses

sistent for all age and sex classes (GLM for Age: $F_{1,214} = 1.10$, $p = 0.30$; for Age \times Rainfall: $F_{1,214} = 0.01$, $p = 0.93$; for Age \times Habitat: $F_{1,214} = 1.50$, $p = 0.22$; for Sex: $F_{1,214} = 1.06$, $p = 0.31$; for Sex \times Rainfall: $F_{1,214} = 0.07$, $p = 0.79$; for Sex \times 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. 5A,C). 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 d since 1 April for mangrove; 36 ± 1 d since 1 April for scrub; mean \pm SE; for 2005: $\chi^2 = 3.85$, $p = 0.04$, $n = 30$; 32 ± 2 d since 1 April for mangrove; 38 ± 2 d 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. 5B), 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 d since 1 April for man-

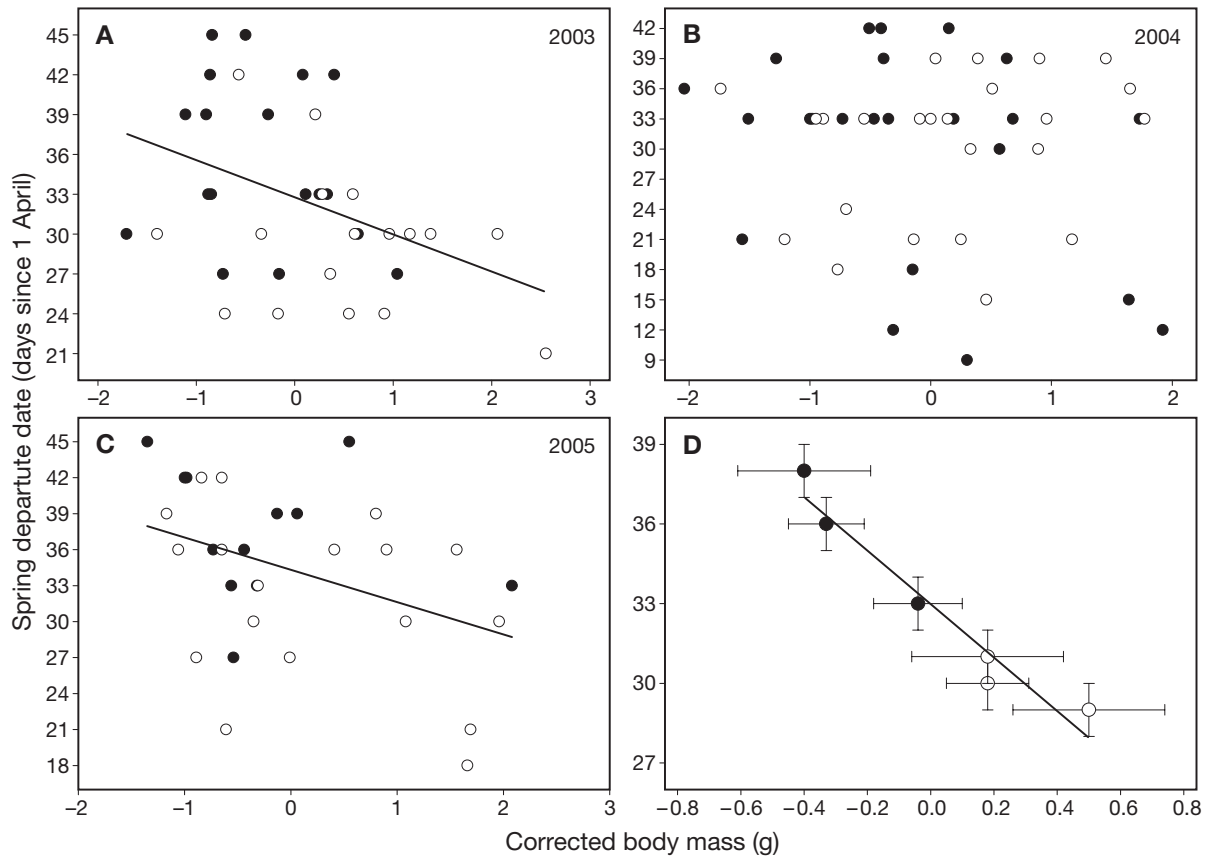


Fig. 5. *Setophaga ruticilla*. (A–C) Relationship between the corrected body mass (mass adjusted for unflattened wing chord, tail length, and tarsus size) of American redstarts in mangrove forest (open circles) and second-growth scrub (filled circles) and their timing of departure on spring migration (mean \pm SE) in each year from 2003 to 2005 at a nonbreeding site in Jamaica, West Indies. (D) Relationship between corrected body mass (mean \pm SE) and the timing of departure on spring migration (mean \pm SE) averaged for all birds in each habitat in each year shown in Panels A to C

grove; 30 ± 2 d since 1 April for scrub). When departure schedules from all 3 yr 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. 5D).

4. 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 (Saino et al. 2004, 2007, this issue, Gordo et al. 2005, Both et al. 2006). 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 & Sherry 2006). Our results indicate that annual shifts in nonbreeding season rainfall influence food availability for American 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 3 out of 4 yr, 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 the dry season accurately predicted their migratory departure dates. Although total dry-season rainfall in 2003 was over 3 times that 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 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. 2004) 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 & 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 11 yr, 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 50 yr (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 indicate 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 (authors' unpubl. data). Because dry-season rainfall in Jamaica is also becoming increasingly variable, such pressures could lead to annually shifting adaptive peaks for body size rather than to sustained directional selection (Grant & 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 & Sherry 2006) and individual upgrade experiments with redstarts (Studds & 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, this issue).

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 & Sutherland 1994, Runge & Marra 2005), and to population management (Almaraz & Amat 2004).

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