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Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird

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Climatic warming has intensified selection for earlier reproduction in many organisms, but potential constraints imposed by climate change outside the breeding period have received little attention. Migratory birds provide an ideal model for exploring such constraints because they face warming temperatures on temperate breeding grounds and declining rainfall on many tropical non-breeding areas. Here, we use longitudinal data on spring departure dates of American redstarts (*Setophaga ruticilla*) to show that annual variation in tropical rainfall and food resources are associated with marked change in the timing of spring departure of the same individuals among years. This finding challenges the idea that photoperiod alone regulates the onset of migration, providing evidence that intensifying drought in the tropical winter could hinder adaptive responses to climatic warming in the temperate zone.

Keywords: American redstart; climate change; ecological constraint; microevolution; phenotypic plasticity; *Setophaga ruticilla*

1. INTRODUCTION

Climatic warming at temperate latitudes is intensifying selection for earlier reproduction in numerous plants and animals [1–3]. Adaptation to novel selective pressures can proceed through two general but non-exclusive mechanisms: populations can undergo microevolution at the genetic level or can adjust through the aggregate effects of individual phenotypic plasticity. Most efforts to gauge the relative importance of these mechanisms for adaptation to changing climate have focused on the narrow time window surrounding reproduction [4,5]. Yet, the timing of reproduction is determined not only by local climate and other factors during this period, but also by events in preceding life-history stages [4,6]. Conditions outside of the breeding period such as habitat quality and resource availability, and other factors such as evolutionary canalization of traits could either facilitate or limit adaptive responses to selection for earlier reproduction [7–9]. The outcome of these factors on reproductive phenology later in the year may also vary annually in relation to aspects of climate that are indirectly related to but distinct from temperature, including snowpack and rainfall [10,11].

Long-distance bird migration systems have served a useful model for documenting responses to changing climate and are highly suited to the task of understanding how climate and life-history traits outside of the breeding period may shape adjustment to selection for earlier breeding. Even in the absence of climatic warming, early arrival in spring enhances reproductive output of both male and female migrants [12,13]. In addition, many of these species now face potentially contrasting environmental changes during different periods of the annual cycle. Simultaneous to warming trends on

temperate breeding grounds, rainfall in tropical non-breeding areas is changing dramatically, declining sharply in many regions and rising modestly in others [14]. Life-history traits important during the non-breeding period, such as the timing of departure on spring migration, may be expected to depend on rainfall because food resources needed to prepare for migration vary in relation to this aspect of climate [15].

However, the idea that changing climate in the tropics could modify the phenology of migration has received little attention because endogenous clocks synchronized to seasonal changes in photoperiod are thought to rigidly control transitions between different phases of the year [16]. This mechanism is considered to be particularly important for the timing of spring migration in species than winter in the tropics because potential seasonal environmental cues are thought to be too weak or unpredictable to reliably stimulate migratory behaviour [17,18]. Two recent studies suggest that tropical precipitation may vary enough to influence the timing of spring arrival. Individual barn swallows (*Hirundo rustica*) arrived earlier at breeding sites in years when the normalized difference vegetation index (NDVI) was high on non-breeding grounds in western Africa and at staging areas north of the Sahara desert [11,19]. Because positive NDVI values signal elevated primary productivity, these studies reasoned that increased food resources owing to high rainfall helped birds depart earlier from non-breeding or staging sites and arrive sooner at breeding grounds. These results indicate that direct estimates of bird responses to rain and food resources are needed to understand how non-breeding events could shape adjustment to climatic warming in the breeding period.

We compiled a longitudinal dataset of spring departure schedules for American redstarts (*Setophaga ruticilla*) at a non-breeding site in Jamaica in two habitats: mesic, black mangrove forest and xeric, second-growth scrub. This

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species is a long-distance Neotropical–Nearctic migratory bird that is widespread on its breeding grounds in North America and throughout its non-breeding range in the Caribbean basin. Male and female redstarts defend exclusive territories throughout the non-breeding period until they depart on spring migration in April–May, and both sexes show strong fidelity to sites occupied in past years [20]. These behaviours make it relatively easy to document spring departure of the same colour-ringed birds over multiple years. We tested the hypothesis that annual variation in tropical rainfall can modify the timing of departure on spring migration of individual redstarts by changing the availability of arthropods consumed as prey.

2. MATERIAL AND METHODS

Fieldwork was done from 2003 to 2009 in southwestern Jamaica at the Font Hill Nature Preserve (18°02' N, 77°57' W) on five 5 ha long-term study plots. Three plots were dominated by black mangrove (*Avicennia germinans*), but also contained some white (*Laguncularia racemosa*) and red mangroves (*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 three plots were characterized by invasive second-growth thorn scrub. This habitat consisted mainly of logwood trees (*Haematoxylon campechianum*), but also had other less common species, including *Bursera simarubra*, *Terminalia latifolia* and *Crescentia alata*. Small pools of water formed in sections of scrub habitat after periods of heavy rainfall, but were present for only several days. All plots were gridded at 25 m intervals to aid the location of redstarts and mapping of their territories.

Throughout each year (15 January–15 April), redstarts were captured in mist nets, aged and sexed, fitted with a unique colour scheme of plastic leg rings and numbered aluminium rings, measured for body size and weighed to the nearest 0.1 g. We delineated the territories of all colour-ringed redstarts that resided on study plots by following each bird for a minimum of 3 person-hours and recording their movements on gridded maps of study plots. We searched these territories every 3 days from 1 April to 15 May in order 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 vocalizations for five bouts of 20 s interspersed with 30 s of silence. We considered birds to have left their territories when the playback drew no response.

We estimated the biomass of arthropods available as redstart prey on a subset of territories during spring of each year (15 March–15 April). This period encompasses the month immediately before birds begin departing their territories. Arthropods sampled during this time should thus reflect the food resources on which individuals rely to prepare for migration. The sweep net was fastened to a 5 m extension pole, allowing arthropods to be sampled from within the average foraging height range of redstarts. One observer made 20 passes of a sweep net over green vegetation while walking a spiral route from the centre to the boundary of the territory. The contents of the sweep net were then overturned into a plastic bag and placed overnight in a freezer (–10°C), preserved in 70 per cent ethanol, and later dried at 50°C for 24 h. All arthropods between 2 and 20 mm in

length that are typically found in redstart regurgitation and faecal samples were weighed (± 0.1 mg) to yield a single measure of food availability on each territory [21].

We acquired monthly rainfall data from the Jamaican Meteorological Service (<http://www.metservice.gov.jm>) for the Burnt Savannah climate monitoring station, which lies roughly 20 km to the northwest of Font Hill and experiences similar amounts of precipitation. For the analysis of spring departure schedules, we focused on annual variation in dry season rainfall (January–March) for the period of 2003–2009, the duration of the present study, because precipitation during these months is a strong predictor of food availability prior to spring migration [15]. To place recent trends within a broader historical context, we also examined directional change in both the total amount and the coefficient of variation in dry season rainfall from 1994 to 2009, the period of long-term research on redstarts at this site.

We fit a Cormack–Jolly–Seber model in program MARK to estimate the probability of successfully resighting redstarts prior to their estimated date of departure [22]. Data on spring departure schedules were then analysed by using a linear mixed model with random intercepts fit for each bird to account for the fact that all individuals were sampled in more than 1 year. The full model contained fixed effects for sex of the territory holder, habitat occupancy, rainfall and each two-way interaction. We restricted our analysis to adults because juveniles tend to leave comparatively late on their first spring migration, and such age-specific differences, coupled with annual variation in number of juveniles in the population, could have biased our ability to detect longitudinal change in departure dates. To identify the time period during which rainfall was best correlated with spring departure, we initially evaluated four models: one with total rainfall from January to March, one with rainfall in January, one with rainfall in February and one with rainfall in March. We used small-sample Akaike's information criteria (AIC) weights (w_i) to select the best-fit model given the data and then used this model to evaluate predictors of departure timing. We assessed the significance of each variable by iteratively removing it from the full model and comparing the reduced to the full model by using a likelihood ratio test with one degree of freedom.

To test the null hypothesis that redstarts use endogenous mechanisms entrained to photoperiod to time their spring departure, we fit a null model containing fixed effects for sex, habitat and their interaction, reasoning that reliance on endogenous cues would lead to uniform departure dates among years after accounting for variation owing to bird demography. We used a likelihood ratio test with two degrees of freedom to compare this model against the full model. We also quantified the intra-class correlation coefficient (ICC) to evaluate the variation in migration schedules that was not explained by bird demography and rainfall, but was instead owing to the ability of birds to repeat their departure date each year.

We used the same model selection approach described above to identify the rainfall model that best fit the data on arthropod biomass in spring. For the retained model, patterns of arthropod biomass on each territory were analysed by using a linear mixed model with random intercepts for each bird and fixed effects for sex of the territory holder, habitat occupancy, rainfall and each two-way interaction. To directly assess how annual change in arthropod biomass shaped the onset of spring migration, we refit the model for

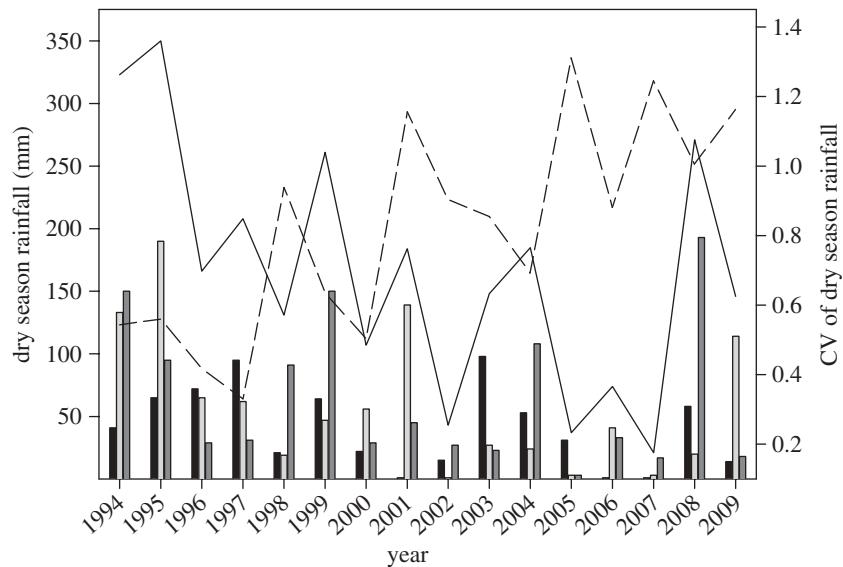


Figure 1. Patterns of dry season rainfall (January–March) from 1994 to 2009 at the Burnt Savannah climate monitoring station in southwestern Jamaica, approximately 20 km from the non-breeding site where American redstarts were studied. The total amount of rainfall in each month is given for January (black bars), February (light grey bars), and March (dark grey bars). The solid line depicts the declining trend in total dry season rainfall and the dashed line shows the increasing coefficient of variation of dry season rainfall.

departure timing with arthropod biomass as a fixed effect and tested its effect by using a likelihood ratio test with one degree of freedom. All analyses were done with program R [23].

3. RESULTS

Precipitation in Jamaica is highly seasonal, with consistent rainfall from September to November and a pronounced dry season from January to March. Over the past 16 years, the dry season has become both increasingly severe and unpredictable, leading to a 11 per cent drop in total rainfall ($r = 0.532$, $p = 0.034$, $n = 16$; figure 1), and a 5 per cent increase in the coefficient of variation of rainfall during the three-month annual drought ($r = 0.563$, $p = 0.008$, $n = 16$; figure 1). During the 6 years considered in the present study, dry season rainfall ranged from a record low of 21 mm in 2007 to a high of 271 mm in 2008, the second highest amount on record.

We recorded 194 departure events for 74 redstarts (32 in mangrove, 42 in scrub). Resight probability during the 45-day spring departure period was reasonably high ($p = 0.819 \pm 0.006$ s.e.; 95% CI: 0.807–0.831). Approximately 57 per cent of birds were monitored for departure in two successive years, and the remaining 43 per cent were followed for between 3 and 6 years (table 1). Individual redstarts changed their date of spring departure from one year to the next based on the amount of rainfall in March ($w_i = 0.938$) rather than in response to rainfall in January ($w_i = 0.003$), February ($w_i = 0.000$) or during the entire January–March ($w_i = 0.059$) dry season (March rain: $\chi^2 = 11.84$, d.f. = 1, $p < 0.001$).

Redstarts overwintering in mangrove forest departed in advance of those inhabiting second-growth scrub (habitat: $\chi^2 = 5.94$, d.f. = 1, $p = 0.015$). Individuals in mangrove delayed their departure on spring migration by 0.8 days for every 50 mm annual reduction in March rainfall, equivalent to a 3-day change in departure across the 6 years

Table 1. Sample sizes of American redstarts used to assess longitudinal change in spring departure dates in relation to dry season rainfall at a non-breeding site in Jamaica, West Indies. Values are the number of years that longitudinal data on spring departure were available for birds in each yearly cohort. Numbers to the left of the slash are sample sizes for redstarts with territories in mangrove forest and those to the right are sample sizes for birds in second-growth scrub. Birds were not monitored for departure in 2006.

year	number of years monitored for spring departure				
	2	3	4	5	6
2003	5/5	2/6	2/0	0/1	1/0
2004	4/9	2/2	1/1	2/1	—
2005	3/1	1/1	1/0	—	—
2007	3/3	1/6	—	—	—
2008	6/4	—	—	—	—
2009	—	—	—	—	—
total	21/22	6/15	4/1	2/2	1/0

during which rainfall fluctuated by 190 mm (mangrove: $\beta = -0.016 \pm 0.007$ s.e.; figure 2a). On average, birds in scrub left on migration 1 day later for each 50 mm reduction in rainfall, equivalent to a 5-day change in departure across all 6 years (scrub: $\beta = -0.025 \pm 0.007$ s.e.; habitat \times rain: $\chi^2 = 0.36$, d.f. = 1, $p = 0.550$; figure 2b). Male redstarts also departed ahead of females, but this pattern did not vary between habitats (sex: $\chi^2 = 10.24$, d.f. = 1, $p = 0.001$; habitat \times sex: $\chi^2 = 1.12$, d.f. = 1, $p = 0.291$; figure 2a,b). Despite this demographic variation in the onset of migration, birds of both sexes changed their departure similarly in relation to annual variation in rainfall (sex \times rain: $\chi^2 = 0.39$, d.f. = 1, $p = 0.534$).

The long-held idea that endogenous timing mechanisms regulate the onset of migration provides a powerful null hypothesis against which to judge the biological

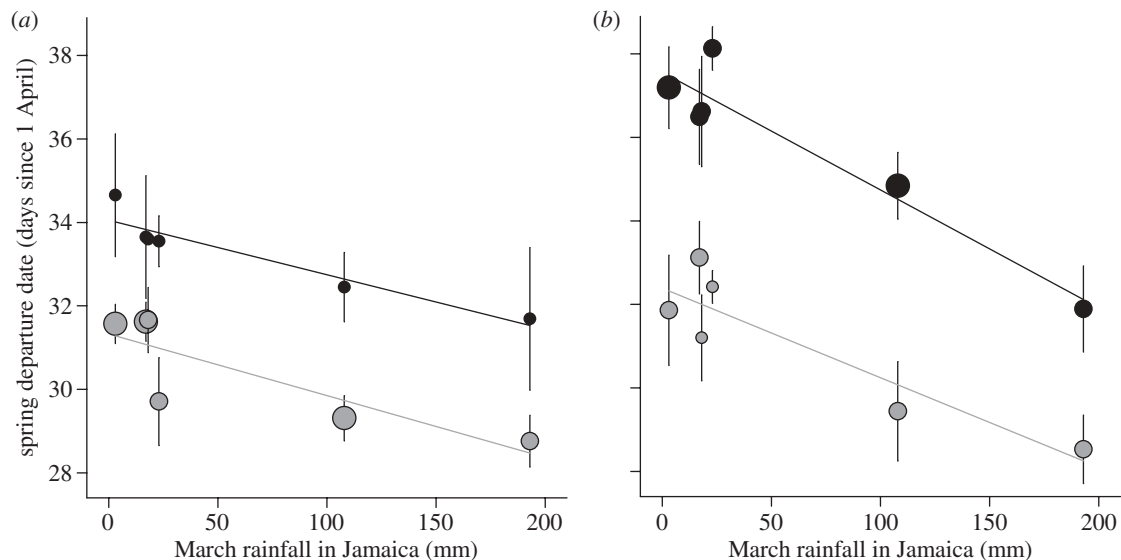


Figure 2. Spring departure dates of 74 American redstarts monitored for 2–6 years to examine longitudinal change in the onset of migration in relation to March rainfall in (a) black mangrove forest and (b) second-growth scrub at a non-breeding site in Jamaica. Data points (mean \pm s.e.) are predicted values from a linear mixed model with non-breeding habitat occupancy, sex of the territory holder, March rainfall and their two-way interactions and are scaled relative to sample size (small: \geq five samples, medium: 6–10, large: 11–15). Although male redstarts (grey symbols) left consistently ahead of females (black symbols), both sexes experienced similar longitudinal change in departure.

significance for environmentally induced variation in spring departure timing. The best model for departure timing, which included effects for habitat, sex, March rainfall and their two-way interactions, fit the data better than the null model that included effects for sex, habitat and their two-way interaction ($\chi^2 = 18.90$, d.f. = 3, $p < 0.001$), providing strong support for the hypothesis that annual variation in rainfall can modify the onset of spring migration. Still, roughly 38 per cent of the variation in departure could not be attributed to bird demography and annual variation in rainfall, indicating some repeatability in the timing of spring departure (ICC = 0.382; 95% CI: 0.247–0.434).

To determine whether annual variation in rainfall facilitated longitudinal change in departure timing by altering the amount of food available to fuel migration, we collected 132 sweep net samples of arthropods on redstart territories in late spring. Arthropod biomass varied in relation to the amount of rainfall in March ($w_i = 0.995$), but did not depend on rainfall in January ($w_i = 0.000$), February ($w_i = 0.000$) or across the full January–March ($w_i = 0.005$) dry period. Arthropods biomass was greatest in years when March rainfall was high and fell at a rate $3.5 \text{ mg } 50 \text{ mm}^{-1}$ annual decline in rainfall (rain: $\beta = -0.070 \pm 0.028$ s.e.; $\chi^2 = 6.34$, d.f. = 1, $p < 0.012$). Arthropod biomass was also greater in mangrove forest than in second-growth scrub, but not in the territories of males compared with females (habitat: $\chi^2 = 11.84$, d.f. = 1, $p < 0.001$; sex: $\chi^2 = 0.05$, d.f. = 1, $p < 0.815$; habitat \times sex: $\chi^2 = 0.64$, d.f. = 1, $p = 0.424$). These differences remained consistent across years that varied in March rainfall (habitat \times rain: $\chi^2 = 1.54$, d.f. = 1, $p = 0.215$; sex \times rain: $\chi^2 = 0.28$, d.f. = 1, $p = 0.868$).

When we included arthropod biomass on each territory in the model for departure timing, we found that it improved overall model fit ($\Delta\text{AIC} = 3.5$; arthropod biomass: $\chi^2 = 8.63$, d.f. = 1, $p = 0.003$). On average,

redstarts in mangrove forest experienced a 1-day delay in departure for each 9.2 mg reduction in arthropod biomass (mangrove: $\beta = -0.109 \pm 0.040$ s.e.; figure 3a). The departure dates of birds in scrub were more sensitive to annual change in arthropod biomass, with a 1-day delay in departure for every 3.5 mg decline in biomass ($\beta = -0.298 \pm 0.092$ s.e.; habitat \times arthropod biomass: $\chi^2 = 0.65$, d.f. = 1, $p = 0.419$; figure 3b). These patterns held for males and females alike (sex \times arthropod biomass: $\chi^2 = 1.22$, d.f. = 1, $p = 0.270$).

4. DISCUSSION

Our results support the hypothesis that environmental conditions on tropical non-breeding areas can modify endogenous timing mechanisms to change the timing of departure on spring migration. Had redstarts relied on endogenous cues alone to schedule their spring departure, all birds would have left their territories at the same time each year after accounting for variation owing to sex and habitat occupancy. Instead, we found that the same birds changed their spring departure from one year to the next in relation to the amount of rainfall in March. Regardless of sex, redstarts in both xeric, second-growth scrub and mesic, mangrove forest delayed spring migration by 3–5 days when drought conditions prevailed. Photoperiod change has been shown experimentally to provide the ultimate cue for migratory activity, and its influence undoubtedly underlies much of the geographical variation in spring departure phenology, especially across latitude [16,24]. However, because we detected similar longitudinal change in the onset of spring migration in males and females and for birds in habitats that differ widely in quality, it is possible that environmental modification of spring departure is common across the non-breeding range of this species.

The correlation between arthropod biomass and the timing of departure suggests annual variation in food

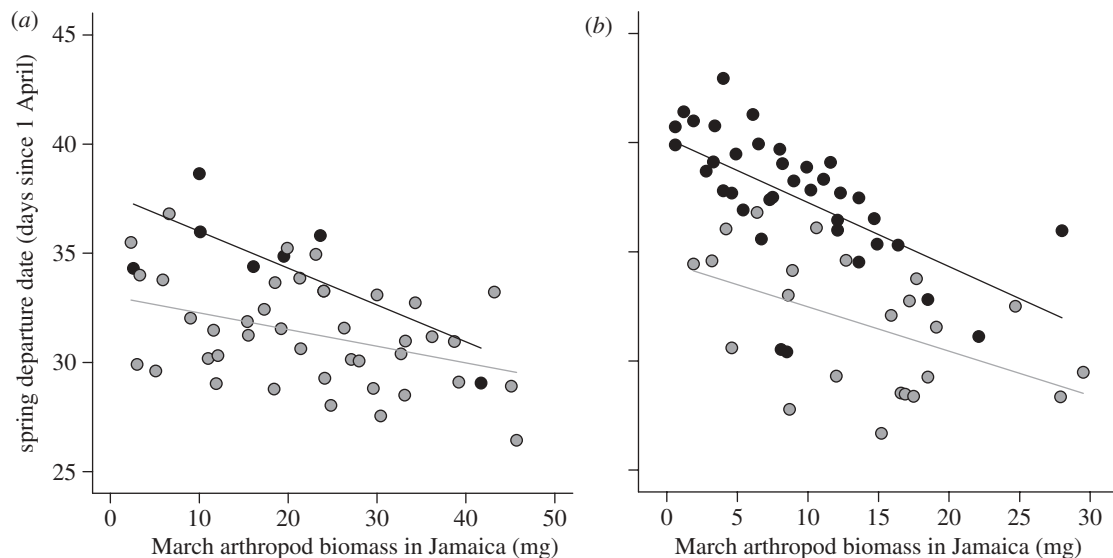


Figure 3. Relationship between longitudinal spring departure dates of 74 American redstarts and the biomass of arthropods available as prey collected from 132 sweep net samples roughly one month before migration in (a) mangrove forest and (b) second-growth scrub at a non-breeding site in Jamaica. Data points are predicted values from a linear mixed model with non-breeding habitat occupancy, sex of the territory holder, March rainfall and their two-way interactions. Both males (grey symbols) and females (black symbols) changed their departure dates each year in relation to arthropod biomass, suggesting food availability as a mechanism underlying the onset of migration.

availability as an important determinant of the redstart spring migration programme. Rainfall in March was better predictor of both food availability and departure timing compared with rainfall during the previous months of the dry season, indicating a resource bottleneck roughly one month before the onset of spring migration. Previous research in this system showed that food-limited birds delayed their departure owing to low body mass [15]. In addition, redstarts provided with experimental territory vacancies moved from food-poor scrub sites to food-rich mangrove ones and departed earlier on spring migration compared with those that remained in scrub [25]. These findings and the results of the present study support the idea that annual variation in food availability can fine-tune the spring departure programme in this species. In years when food availability is high, redstarts may be able to follow an optimal spring departure schedule, relying primarily on endogenous timing mechanisms synchronized to photoperiod. Conversely, in years where drought conditions exist, low food availability may prevent exclusive use of photoperiod to cue departure.

A critical question is whether this variation in the onset of spring migration carries fitness consequences. Delaying spring departure when food resources are low might be adaptive because undertaking migration without first storing adequate body reserves may reduce survival probability during migration, the period of the annual cycle with the highest mortality risk for migratory birds [26]. However, the same delay in departure could be costly for reproduction. Most redstarts arrive on breeding grounds within 14 days of one another, so a 3–5 day delay in winter departure could translate to a 20–35% delay in arrival. In Ontario, male redstarts that lagged the earliest arrivals by 3–5 days fledged 0.4–0.6 fewer offspring per summer owing to less time to replace failed clutches with social mates and fewer opportunities to sire extra-pair young [13]. Comparable estimates are unavailable for females, but early arrival in females is

associated with earlier clutch initiation dates, larger clutch sizes and heavier offspring at fledging, all of which are correlated with high reproductive success [27,28]. Stable-carbon isotopes in bird tissues indicate that arrival date and reproductive output are enhanced by occupancy of food-rich habitats in the previous winter [12,13]. Although it is difficult to use spatial patterns to predict temporal responses, it is possible that annual variation in rain and food resources could induce variation in reproductive success for the same birds over multiple years. This idea is supported by past research with both Palaeotropical and Neotropical migrants, where arrival date on breeding grounds and reproductive success depended in part on rainfall or allied climate cycles in the non-breeding period [11,19,29].

Redstarts could offset these potential reproductive costs by adjusting the pace of spring migration. For migratory birds, long-term warming trends on migration routes are thought to have facilitated phenotypic plasticity for earlier breeding [5,30]. Once they cross geographical barriers such as deserts or oceans, birds may adjust the pace of migration to match ambient temperatures or related factors such as leaf emergence and tail winds from warm fronts [31–33]. Because adult redstarts show site fidelity to the latitude of their first breeding attempt, the ability to modulate the speed of migration might help returning adults remain in synchrony with phenology at past breeding sites when poor winter conditions force late departure [34]. Although temperatures have warmed nearly 0.5°C per decade in eastern North America over the last 40 years, redstarts have not arrived earlier at migration ringing stations [33,35]. This suggests that the redstart spring migration programme is currently dominated by both endogenous timing mechanisms and resource constraints during the tropical non-breeding period. This situation contrasts with that for Palaeotropical migrants, where spatial and temporal variations in en route temperatures are stronger predictors of breeding ground arrival than conditions on non-breeding areas [36].

It has also been argued that advancement in breeding ground arrival dates in Palaetropical migrants has occurred though rapid microevolution [37]. Support for this idea is based on phenotypic changes in breeding ground arrival time and evidence for high additive genetic variation in traits associated with the phenology of spring migration [7,38]. Even though inter-annual differences in rain and food resources explained much of the change in redstart departure among years, individuals still showed a 38 per cent repeatability of migration timing. This response probably represents the variation in departure owing to endogenous timing mechanisms, but might also arise from an ability to time departure to match past breeding latitude [39]. Yet, the considerable variation in repeatability among individuals suggests that departure timing may also show some genetic variation (95% CI: 0.247–0.434). There is currently no evidence for genetic variation of migratory traits in redstarts, but heritability of such traits could facilitate microevolution of departure timing if a repeatable migration schedule enhances survival or reproduction.

The 11 per cent drying trend we report for Jamaica spans only 16 years, yet it appears to be a widespread phenomenon throughout the Caribbean, the centre of the non-breeding range for many Neotropical–Nearctic migratory birds. For example, rainfall at the Luquillo Experimental Forest in northeastern Puerto Rico fell by 5 per cent from 1998 to 2003 [40]. In the Bahamas, rainfall declined by roughly 10 per cent on Inagua Island from 1959 to 1990 and by nearly 14 per cent on Long Island [41]. These data are in line with model predictions of increasingly severe drought in the Caribbean over the next 50 years [14]. Although such directional shifts are a hallmark of climate change, increased variance in environmental conditions is also predicted [42]. Accompanying the decline in dry season rainfall in Jamaica has been a 5 per cent increase in the coefficient of variation during the same period of the year. Thus, although the dry season in south-western Jamaica is becoming more severe, it is also growing more unpredictable, with stereotypical patterns of drought from January to March in some years and a complete reversal of this pattern in others. Birds and other organisms migrating between the Caribbean and North America must thus contend with fewer and more variable winter food resources, while at the same time attempting to breed earlier in a warming temperate zone. Understanding how birds will respond to these conflicting challenges will require a more integrated understanding of the correlations and trade-off among phenotypic traits in different phases of the annual cycle and detailed demographic monitoring of multiple species.

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REFERENCES

- Møller, A. P., Rubolini, D. & Lehikoinen, E. 2008 Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl Acad. Sci. USA* **105**, 16 195–16 200. (doi:10.1073/pnas.0803825105)
- Arft, A. M. *et al.* 1999 Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.* **69**, 491–511.
- Frick, W. F., Reynolds, D. S. & Kunz, T. H. 2010 Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J. Anim. Ecol.* **79**, 128–136. (doi:10.1111/j.1365-2656.2009.01615.x)
- Post, E. S., Pedersen, C., Wilmers, C. C. & Forchhammer, M. C. 2008 Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* **89**, 363–370. (doi:10.1890/06-2138.1)
- Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merila, J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178. (doi:10.1111/j.1365-294X.2007.03413.x)
- Marra, P. P., Hobson, K. A. & Holmes, R. T. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886. (doi:10.1126/science.282.5395.1884)
- Pulido, F. 2007 Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Clim. Res.* **35**, 5–23. (doi:10.3354/cr00711)
- Bonenfant, C. *et al.* 2009 Empirical evidence of density dependence in populations of large herbivores. In *Advances in ecological research*, vol. 41 (ed. H. Caswell), pp. 313–357. Burlington, MA: Academic Press.
- Reudink, M. W., Studds, C. E., Marra, P. P., Kurt Kyser, T. & Ratcliffe, L. M. 2009 Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. *J. Avian Biol.* **40**, 34–41. (doi:10.1111/j.1600-048X.2008.04377.x)
- Inouye, D. W., Morales, M. A. & Dodge, G. J. 2002 Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. *Oecologia* **130**, 543–550. (doi:10.1007/s00442-001-0835-y)
- Saino, N., Szep, T., Romano, M., Rubolini, D., Spina, F. & Møller, A. P. 2004 Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol. Lett.* **7**, 21–25. (doi:10.1046/j.1461-0248.2003.00553.x)
- Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. & Sutherland, W. J. 2005 Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. R. Soc. B* **272**, 2319–2323. (doi:10.1098/rspb.2005.3214)
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M. & Ratcliffe, L. M. 2009 Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proc. R. Soc. B* **276**, 1619–1626. (doi:10.1098/rspb.2008.1452)
- Neelin, J. D., Munnich, M., Su, H., Meyerson, J. E. & Holloway, C. E. 2006 Tropical drying trends in global warming models and observations. *Proc. Natl Acad. Sci. USA* **103**, 6110–6115. (doi:10.1073/pnas.0601798103)
- Studds, C. E. & Marra, P. P. 2007 Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Clim. Res.* **35**, 115–122. (doi:10.3354/cr00718)
- Gwinner, E. 1986 *Cirannual rhythms: endogenous clocks in the organization of seasonal processes*. University of California: Springer.
- Both, C. & Visser, M. E. 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296–298. (doi:10.1038/35077063)

- 18 Coppack, T. 2007 Experimental determination of the photoperiodic basis for geographic variation in avian seasonality. *J. Ornithol.* **148**, S459–S467. (doi:10.1007/s10336-007-0158-9)
- 19 Balbontin, J., Moller, A. P., Hermosell, I. G., Marzal, A., Reviriego, M. & de Lope, F. 2009 Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *J. Anim. Ecol.* **78**, 981–989. (doi:10.1111/j.1365-2656.2009.01573.x)
- 20 Marra, P. P. & Holmes, R. T. 2001 Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk* **118**, 92–104. (doi:10.1642/0004-8038(2001)118[0092:CODMHS]2.0.CO;2)
- 21 Sherry, T. W. & Holmes, R. T. 1997 American redstart (*Setophaga ruticilla*). In *Birds of North America*, vol. 277 (eds A. Poole & F. Gill). Washington, DC: The Academy of Natural Sciences of Philadelphia, Philadelphia, PA and The American Ornithologists' Union.
- 22 White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Suppl.), 120–138. (doi:10.1080/00063659909477239)
- 23 R Core Development Team. 1999 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- 24 Helm, B., Schwabl, I. & Gwinner, E. 2009 Circannual basis of geographically distinct bird schedules. *J. Exp. Biol.* **212**, 1259–1269. (doi:10.1242/jeb.025411)
- 25 Studds, C. E. & Marra, P. P. 2005 Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology* **86**, 2380–2385. (doi:10.1890/04-1145)
- 26 Sillett, T. S. & Holmes, R. T. 2002 Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* **71**, 296–308. (doi:10.1046/j.1365-2656.2002.00599.x)
- 27 Smith, R. J. & Moore, F. R. 2005 Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behav. Ecol. Sociobiol.* **57**, 231–239. (doi:10.1007/s00265-004-0855-9)
- 28 Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. & Ratcliffe, L. M. 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. R. Soc. Lond. B* **271**, 59–64. (doi:10.1098/rspb.2003.2569)
- 29 Sillett, T. S., Holmes, R. T. & Sherry, T. W. 2000 Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* **288**, 2040–2042. (doi:10.1126/science.288.5473.2040)
- 30 Przybylo, R., Sheldon, B. C. & Merila, J. 2000 Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69**, 395–403. (doi:10.1046/j.1365-2656.2000.00401.x)
- 31 Kemp, M. U., Shamoun-Baranes, J., van Gasteren, H., Bouten, W. & van Loon, E. E. 2010 Can wind help explain seasonal differences in avian migration speed? *J. Avian Biol.* **41**, 672–677. (doi:10.1111/j.1600-048X.2010.05053.x)
- 32 Smith, R. J., Mabey, S. E. & Moore, F. R. 2009 Spring passage and arrival patterns of American redstarts in Michigan's eastern upper peninsula. *Wilson J. Ornithol.* **121**, 290–297. (doi:10.1676/08-051.1)
- 33 Marra, P. P., Francis, C. M., Mulvihill, R. S. & Moore, F. R. 2005 The influence of climate on the timing and rate of spring bird migration. *Oecologia* **142**, 307–315. (doi:10.1007/s00442-004-1725-x)
- 34 Studds, C. E., Kyser, T. K. & Marra, P. P. 2008 Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proc. Natl Acad. Sci. USA* **105**, 2929–2933. (doi:10.1073/pnas.0710732105)
- 35 Karl, T. R., Melillo, J. M. & Petersen, T. C. (eds) 2009 *Global climate change impacts in the United States*. Cambridge, UK: Cambridge University Press.
- 36 Both, C. 2010 Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Curr. Biol.* **20**, 243–248. (doi:10.1016/j.cub.2009.11.074)
- 37 Jonzen, N. *et al.* 2006 Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **312**, 1959–1961. (doi:10.1126/science.1126119)
- 38 Berthold, P. & Pulido, F. 1994 Heritability of migratory activity in a natural bird population. *Proc. R. Soc. Lond. B* **257**, 311–315. (doi:10.1098/rspb.1994.0131)
- 39 Conklin, J. R., Battley, P. F., Potter, M. A. & Fox, J. W. 2010 Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nat. Commun.* **1**, 1–6. (doi:10.1038/ncomms1072)
- 40 Heartsill-Scalley, T., Scatena, F. N., Estrada, C., McDowell, W. H. & Lugo, A. E. 2007 Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. *J. Hydrol.* **333**, 472–485. (doi:10.1016/j.jhydrol.2006.09.019)
- 41 Martin, H. C. & Weech, P. S. 2001 Climate change in the Bahamas? Evidence in the meteorological records. *Bahamas J. Sci.* **5**, 22–32.
- 42 Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. & Mearns, L. O. 2000 Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074. (doi:10.1126/science.289.5487.2068)