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The role of tropical rainfall in driving range dynamics for a long-distance migratory bird

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Predicting how the range dynamics of migratory species will respond to climate change requires a mechanistic understanding of the factors that operate across the annual cycle to control the distribution and abundance of a species. Here, we use multiple lines of evidence to reveal that environmental conditions during the nonbreeding season influence range dynamics across the life cycle of a migratory songbird, the American redstart (*Setophaga ruticilla*). Using long-term data from the nonbreeding grounds and breeding origins estimated from stable hydrogen isotopes in tail feathers, we found that the relationship between annual survival and migration distance is mediated by precipitation, but only during dry years. A long-term drying trend throughout the Caribbean is associated with higher mortality for individuals from the northern portion of the species' breeding range, resulting in an approximate 500 km southward shift in breeding origins of this Jamaican population over the past 30 y. This shift in connectivity is mirrored by changes in the redstart's breeding distribution and abundance. These results demonstrate that the climatic effects on demographic processes originating during the tropical nonbreeding season are actively shaping range dynamics in a migratory bird.

climate change | migration | seasonal interactions | species range dynamics | survival

A complex suite of abiotic and biotic factors drive the vital rates that ultimately determine species distributions and range dynamics (1). Climate is a key abiotic factor that is currently changing and altering the distributions of many species globally, and conventional approaches predict poleward range shifts under climate change (2–4). The processes underlying these patterns remain elusive for most species, hindering accurate prediction (5, 6) and potentially providing flawed guidance for climate adaptation and conservation planning (7). Proximate causes of distributional shifts are particularly complex for animals that migrate thousands of kilometers between temperate and tropical regions annually and when conditions experienced in one location can carry over to affect individual performance at later stages (8). Forecasting the consequences of climate change on the distribution and abundance of migratory species therefore requires a rigorous understanding of how events and selective pressures operating throughout the annual cycle influence population dynamics.

Survival is a central determinant of population dynamics and, for migratory species, varies seasonally (9). Threats to survival of migratory birds peak during spring migration (9), largely due to several factors either acting alone or together including physiological stress, weather (10), geographic barriers, and collisions (11). As a result, individuals that travel longer distances may face higher mortality because they are exposed to hazards for longer time periods. These risks may be further exacerbated by environmental conditions (e.g., tropical precipitation) experienced during the nonbreeding period that carry over to influence migratory behavior and differentially impact survival (12, 13). Nonbreeding conditions have the potential to influence population dynamics on the breeding grounds by mediating survival during migration and thus impacting breeding population abundance (14–16). If longer migration distance (i.e., breeding latitude) reduces survival and abundance, then the link between nonbreeding season conditions and migratory behavior may act as an important mechanism influencing species range dynamics (17) as it would imply that northern breeding populations are more strongly influenced by tropical climatic conditions.

Here, we use multiple lines of evidence from long-term data to investigate the role that tropical precipitation plays in mediating species range dynamics indirectly through adult survival during spring migration and its effect on breeding abundance and occupancy. Given the link between tropical precipitation and spring departure and migratory behavior (12, 18, 19), we sought to evaluate the effect that rainfall would have on mediating the effect of migration distance on survival (i.e., cost of migration) by modeling apparent annual survival using mark-resight data (2002 to 2019) from a nonbreeding population of American redstarts in Jamaica. To test the hypothesis that a long-term drying trend throughout the Caribbean (20) influenced breeding range dynamics and migratory connectivity of this Jamaican nonbreeding

Significance

Identifying causal mechanisms underlying species' responses to global change is critical to ecological forecasting and climate adaptation. Here, we demonstrate, using long-term data from a migratory bird, the American redstart, that dry conditions on nonbreeding areas can impose costs to migration that differentially impact individuals migrating greater distances to more northern breeding areas. A long-term drying trend in the Caribbean and subsequent higher mortality of birds breeding in the northern portion of their breeding range have coincided with a southward shift in the breeding distribution of our study population. Our study presents evidence supporting a mechanism of contemporary changes in species distributions under global climate change, which challenges a common view of climate-induced northward range shifts.

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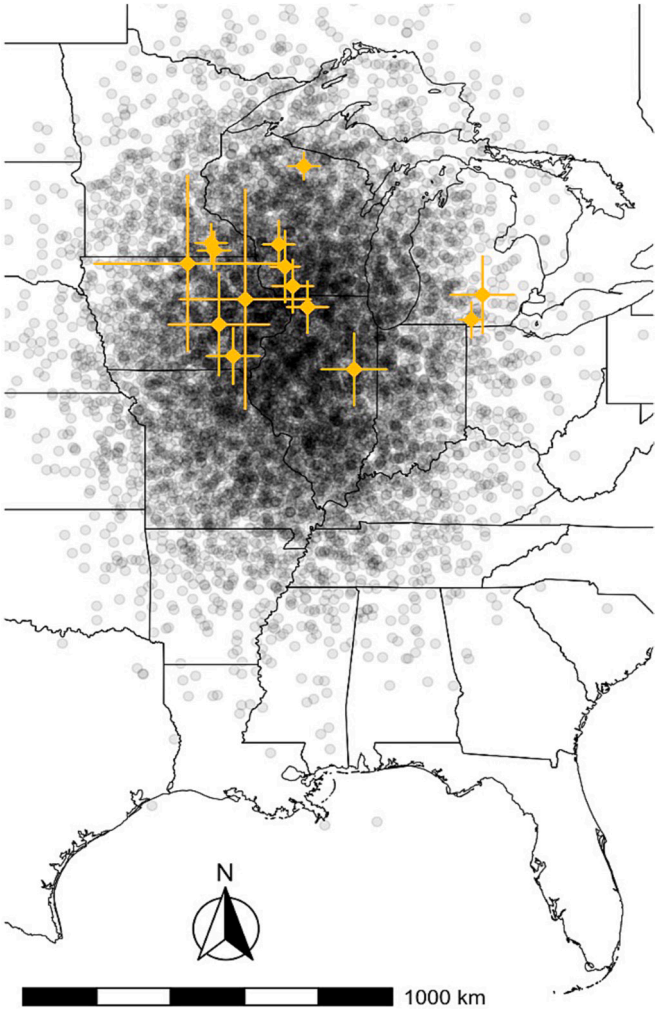

Fig. 1. Probable breeding origins of a nonbreeding population of American redstarts (*Setophaga ruticilla*) that overwinter in southwest Jamaica at the Font Hill Nature, Preserve St. Elizabeth Parish, Jamaica. Gray dots represent simulated breeding locations (latitudes and longitudes) that were drawn randomly from realistic distributions estimated from the two data sources—stable hydrogen isotopes and light-level geolocators, respectively. Darker regions represent the core breeding area of the Jamaican redstarts. Orange diamonds and whiskers represent mean breeding locations (±SE) of individuals equipped with light-level geolocators. Ninety-five percent of the population originates from the 35 to 50°N while the core of the population (50%) originates from the region 38 to 43°N.

population, we evaluated how breeding origin, determined with stable hydrogen isotopes from tail feathers (δH_f), has changed over time (1990 to 2019). We coupled these isotope data with light-level geolocator data from individually tagged birds to delimit the breeding region of our nonbreeding population (Fig. 1) (12). By linking our nonbreeding population to its breeding region, we were able to directly test the mechanism that climate-mediated costs of migration can directly impact breeding bird abundance and occupancy using a Bayesian hierarchical model fit to breeding-season redstart abundance [North American Breeding Bird Survey (BBS), 21]. These data were then used to fit a hierarchical multiseason occupancy model to investigate how these patterns ultimately influence the distribution of redstarts across this nonbreeding population's breeding region.

Results

Based on δH_f values and light-level geolocator analyses, redstarts spending the nonbreeding season in Jamaica had a high probability of breeding in the Upper Midwest region of the United States (Fig. 1, 12). Individuals bred as far north as Ontario to as far south as Alabama with 95% of the population originating from 35° to 50°N and with the core of the population (50%) lying between 38° and 43°N. Migration distances for individuals traveling between Jamaica and their temperate breeding grounds therefore differed by more than 2,000 kms with birds migrating an average 3,000 km to their core breeding region (Fig. 1).

The top survival model included both tropical rainfall (January – March total rain), migration distance (e.g., δH_f), and their interaction (*SI Appendix*, Table S3) after accounting for transience, sex, habitat type, and their respective two-way interactions. Males had significantly higher survival than females ($\beta_{\text{Sex[Males]}} = 1.28$, 95% CI = 0.58, 1.98) and were significantly more likely to be transient ($\beta_{\text{Transience*Sex}} = 1.43$, 95% CI = 0.64, 2.23). Birds occupying higher quality wet mangrove habitat were less likely to be transient ($\beta_{\text{Transience*Habitat}} = -0.97$, 95% CI = −1.76, −0.17). Moreover, the effect of tropical rainfall on male survival was significantly weaker than its effect on female survival ($\beta_{\text{Rain*Sex}} = -0.40$, 95% CI = −0.75, −0.05). After accounting for these effects, we determined that rainy years had a strong positive effect on survival ($\beta_{\text{Rainfall}} = 0.36$, 95% CI = 0.08, 0.64). Migration distance had a negative effect on survival, but this effect was mediated by tropical rainfall (Fig. 2, $\beta_{\text{MigrationDistance*Rainfall}} = -0.09$, 95% CI = −0.27, 0.08). While dry years (rainfall < 74 mm) exacerbated the cost of long-distance migration (Fig. 1B; $\beta_{\text{MigrationDistance*Dry}} = -0.06$, 95% CI = –0.03), wet years (rainfall > 272 mm) dampened it (Fig. 2*A*; $\beta_{\text{Migration Distance*Wet}} = -0.02$, 95% CI = −0.11, 0.07). During wet years, the difference in survival between the longest (0.64 ± 0.10) and shortest distance (0.77 ± 0.06) migrants was only 13%. However, during dry years, the survival of individuals with the longest (0.46 ± 0.12) and shortest (0.83 ± 0.05) migrations differed by approximately 37%. The effects of tropical rainfall on survival are therefore stronger for more northern-breeding redstarts, which migrate-farther, than they are for more southern breeding redstarts.

Consistent with increasing frequency of dry years in Jamaica (*SI Appendix*, Fig. S4) and reduced survival of the longest distance migrants, the breeding origins of redstarts overwintering in Jamaica have shifted south ($\beta_{\text{Year}} = 0.34$, SE = 0.11, $P \ll 0.01$) by more than 500 km since 1990 (Fig. 3 *A* and *C*). This shift in mean breeding latitude (δH_f) was correlated with a loss of northern breeding individuals and an increase in recruitment of southern breeders (Fig. 3*B*). These results are consistent with our survival analysis and point to a significant shift in patterns of migratory connectivity over the past 30 y.

Based on these results, we sought to determine the extent to which tropical rainfall influenced breeding ground abundance. Controlling for the potential effects of breeding conditions (breeding rainfall and temperature; *SI Appendix*, Table S4), we determined that tropical rainfall in Jamaica had a positive effect (*SI Appendix*, Table S4; $\beta_{\text{Rainfal}} = 0.01$, 95% CI = 0.00, 0.03) on the subsequent breeding bird abundance but that this effect increased at more northern latitudes breeding latitude (*SI Appendix*, Table S4; $\beta_{\text{RainfalBreedingLatitude}} = 0.01$, 95% CI = 0.00, 0.03). In fact, the effect of tropical rainfall on breeding bird abundance was nonsignificant at more southernly latitudes and significantly positive at latitudes above 42°N (Fig. 4). These data indicate that nonbreeding conditions exert strong influences on breeding ground population dynamics, especially at the northern range extent.

These patterns in abundance also mirrored changes in the breeding distribution of redstarts on their breeding grounds. We found a significant positive trend in occupancy across BBS routes (*SI Appendix*, Table S6, $\beta_{Year} = 0.65$, 95% CI = 0.26, 1.09).

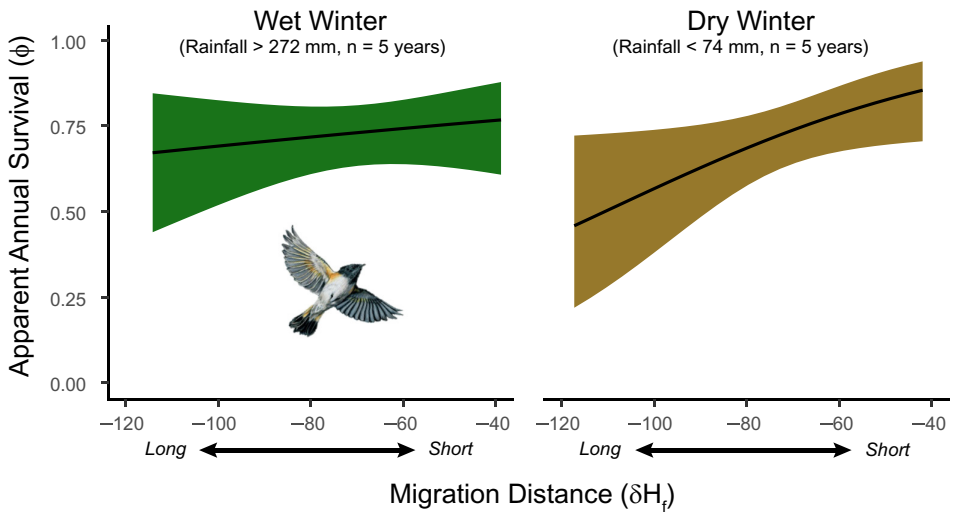

Fig. 2. Migration distance negatively influenced annual survival of American redstarts following dry (*Left*; β = −0.335, 95% CI = −0.608, −0.062) but not wet winters (*Right*; β = −0.042, 95% CI = −0.360, −0.276). Migration distance was inferred from stable-hydrogen isotopes in feathers (δ^2H_f), with more negative values representing higher breeding latitudes, and thus longer migration distances. Dark lines represent the predicted mean survival for individuals of varying migration distances given wet (winter rainfall > 272 mm rain) and dry (winter rainfall < 74 mm rainfall) winters for males residing in mangrove habitat. These patterns are quantitatively similar to females and birds residing in logwood habitat. The shaded region represents the 95% CI envelope of the prediction.

However, changes in occupancy were spatially variable (*SI Appendix*, Fig. S5). While the northern range limit has remained stable over the past 30 y, more southerly breeding populations have increased by over 50% since 1990 (*SI Appendix*, Fig. S5), consistent with a shift in the geographic distribution of abundance and changes in connectivity we observed in Jamaica.

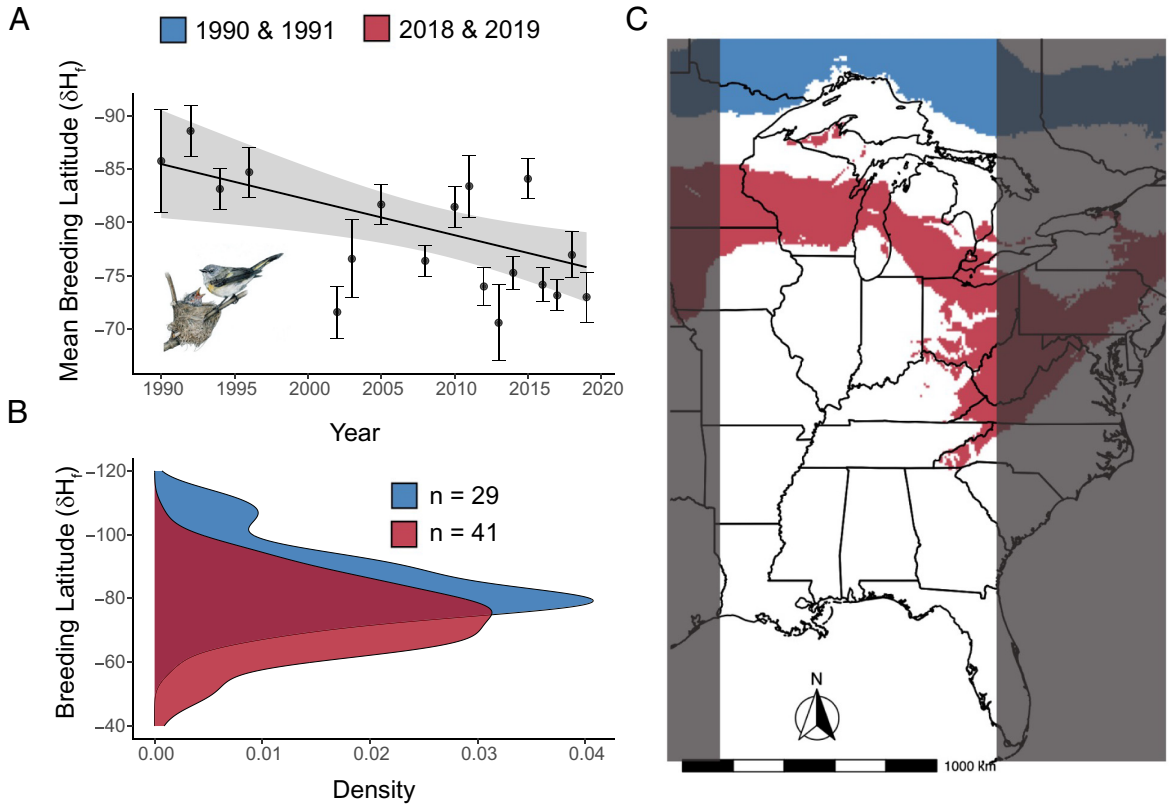

Fig. 3. The breeding origins of the Jamaican overwintering population from 1990 to 2019 have shifted southward by more than 500 km (*A* and *C*), which is driven by the loss of northern breeding individuals and increased recruitment of more southern birds (*B*). Subplot *A* depicts the southward trend in mean breeding origins of our Jamaica population. Each point in subplot (*A*) represents mean δ^2H_f for a given year, and whiskers depict ±1 SE. The slope was calculated using inverse-variance weighted regression to account the variance in mean annual δH_f, and the shaded region represents the 95% CI envelope. Subplot (*B*) highlights the differences in the breeding distribution of our winter population between the start of the study (blue distribution; 1990 & 1991, N = 29) and the most recent years of data (red distribution; 2018 & 2019, N = 41). Subplot (*C*) shows how the mean breeding origin of our population has shifted southward from the start of the study to the present day, taking into account sampling error. It is a visual representation of the geographical changes depicted in Subplot (*B*). Regions shaded in gray demarcate longitudinal bounds outside the 95% confidence band of breeding longitude estimated from light-level geolocators.

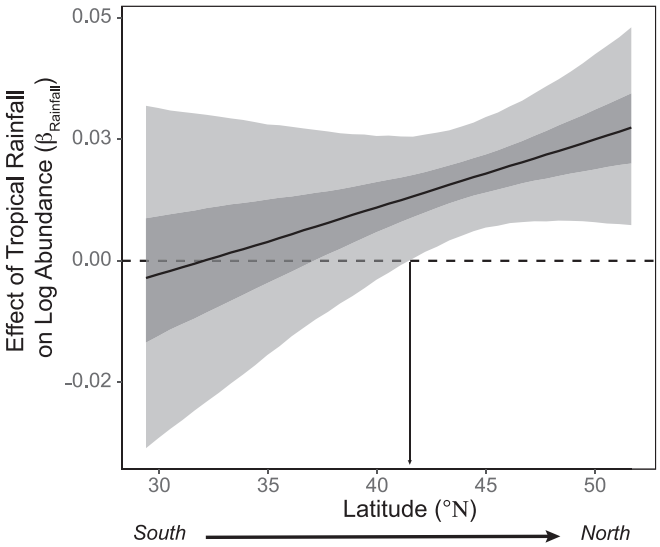

Fig. 4. Tropical rainfall is positively correlated with redstart breeding abundance at northern latitudes (>42°N) but not with breeding abundances at more southernly latitudes. ($\beta_{Rainfall*Latitude}$ = 0.01, 95% CI = 0.00, 0.03). The solid black line represents the mean trend, and the light gray and dark gray regions represent the 95% and 50% credible intervals, respectively. The solid arrow depicts the latitude above which the effect of rainfall is positive and significantly different from 0.

Discussion

Migratory animals experience a myriad of conditions across their annual cycle that affect breeding productivity and survival in subsequent stages to ultimately influence population dynamics (8). These species present a powerful opportunity to improve our understanding of range dynamics by investigating the role that carry-over effects play in mediating population abundance and distributions. Quantifying migratory connectivity provides an important window into how climate patterns impact population and range dynamics (7). Here, we build on previously published evidence of seasonal interactions between tropical rainfall and the timing of migration (8, 19, 22), reproductive success (23, 24), abundance (14), survival (13, 16), and natal dispersal (25) to propose that variation and long-term trends in precipitation on the tropical nonbreeding areas influence population abundance and range dynamics on temperate breeding areas through its effect on the costs of migration.

We demonstrate that the underlying drivers of redstart population dynamics differ across the breeding range and that migration distance, in particular, is an important consideration of contemporary range shifts. Adult survival is a critical component of life history and is particularly important factor influencing population dynamics (26, 27). In fact, although recent analyses (28) have attributed reduced survival of northern breeding individuals to costs of reproduction, our results suggest that these patterns may be mediated by nonbreeding conditions. Adult survival (9, 13) can be strongly influenced by nonbreeding conditions (13, 29) which, subsequently affect population dynamics on breeding grounds (16, 30, 31). Determining how survival ultimately affects populations therefore requires understanding migratory connectivity and how these patterns in survival might differ across populations. Yet the bulk of these studies are conducted on a single population in a single season and therefore have not been able to assess how these relationships differ across a linked species' breeding and nonbreeding range—the relevant areas of inference. In our study population, although the core of our population is centered in the Midwest, individuals originate from as far south as Alabama and as far north as Ontario, allowing us to investigate the critical role that breeding latitude plays in mediating these seasonal interactions.

Like many species, American redstarts face strong time constraints during spring migration because early arrival on breeding sites improves reproductive success (32). Departure on spring migration from tropical nonbreeding sites is delayed in years of low rainfall (19) because reductions in food availability (e.g., insect biomass) limit the ability to build the energy reserves required for optimal migration (18, 19, 33). Given the fitness costs of delayed arrival to breeding grounds (23), individuals potentially adopt riskier migratory strategies to compensate for delays that ultimately lead to reduced survival (12). These risks are likely magnified over longer migrations following dry winters, resulting in significant survival costs on longer distance migrants that breed at more northernly areas. As expected, we found that while populations at the northern margins of the redstart range appear to be limited by winter rainfall, more southerly populations appear to be relatively unaffected. While our conclusions are drawn from a single nonbreeding site, nonbreeding season rainfall impacts on survival and abundance are widespread and have been found in a number of species (11, 23, 24, 28, 34). Our results emphasize that the cost of migration is a plausible mechanism underlying such rainfall effects on population dynamics.

Dispersal and survival are intimately connected in migratory populations, and it is difficult to decompose specific effects on survival without considering dispersal. However, two lines of evidence suggest that the apparent annual survival effects that we observed are driven by differences in survival rather than dispersal. First, redstarts exhibit high winter site fidelity that is on par with breeding site fidelity—with individuals returning to within meters of their previous year's territory (34). Second, while dispersal appears to be relatively common in juveniles, it is relatively rare in adults (14, 35). We propose that same case can be made with nonbreeding dispersal. We also attempted to methodologically limit potential influence of dispersal on our conclusions by restricting analyses to adults and incorporating transience in our survival models. Therefore, our estimates of apparent survival are likely to reflect true patterns in survival and not dispersal.

Over the past 30 y, the breeding origin of redstarts overwintering in Jamaica has shifted south by more than 500 km, a shift in migratory connectivity consistent with changes in occupancy on the breeding grounds. While occupancy has increased by more than 50% within the core of our breeding range, breeding populations at higher latitudes have not grown. We argue that the observed change in occupancy is mainly a consequence of a long-term increase in the frequency of dry seasons in the Caribbean. This rise in dry seasons has disproportionately and negatively affected the survival of individuals breeding in the northern latitudes, which has led to the suppression of population growth rates this region (>43°N), despite the increase in population in the southern latitudes. Although forest cover and breeding rainfall were important factors influencing abundance and occupancy, we found no significant trends in either of these factors that would predict this change in distribution we observed. However, we cannot definitively rule out the potential for unknown competing effects and interactions in driving redstart occupancy trends. Species distributions are influenced by a host of competing effects that may obscure the relationship between patterns of abundance, survival, and distribution. For example, decreased survival of northern populations following a dry nonbreeding season may, in part, be compensated by higher reproductive success via density-dependent mechanisms (36). This

demographic compensation could offset declines of populations at the northern margin of a species range (37) to the point that it would exceed the ability of a population to compensate (35, 37). Although we do not contend that nonbreeding conditions are the sole determinants of a species distribution, our results suggest that they are an important driver of range dynamics especially considering the drastic southward shift of the geographic center of abundance over the past 30 y.

In conclusion, our ability to predict range dynamics and changes in a species distribution in response to future climate scenarios requires that we consider how abiotic and biotic effects throughout the annual cycle differentially affect population dynamics (1, 38). Bioclimatic models used to predict breeding range shifts under future climate scenarios typically focus on breeding season biology. Most conclude that breeding ranges will shift north with rising temperatures (39) without consideration of factors occurring during other seasons (6, 14, 40). Our results emphasize that predicting future breeding distributions for temperate–tropical migratory species requires linking nonbreeding conditions to the appropriate breeding areas. This research required long-term population data from both breeding and nonbreeding areas and the use of intrinsic markers and tracking technology. Ultimately, if declines in tropical rainfall during the nonbreeding season broadly reduces survival of migratory birds breeding at high latitudes, their population dynamics and breeding distributions will shift in ways contrary to forecasts from conventional bioclimatic models.

Materials and Methods

We captured, color banded, and monitored survival of redstarts (19, 41) from 1990 to 2019 in southwestern Jamaica at the Font Hill Nature Preserve in St. Elizabeth Parish (18° 02′ N, 77° 57′ W, <5 m above sea level). Study effort varied considerably from 1990 to 2001, so we limited our mark-resight dataset for subsequent survival analyses to the period between 2002 and 2019 which consisted of 4-mo field seasons with field crews consisting of at least 4 people. All other analyses were conducted using the full 30-y dataset. Before releasing birds, we plucked a tail feather from 421 individuals that we later analyzed for its δH_f value (8, 25, 42). Following, Studds et al. (19), we use January through March total rainfall since it was found to be the best predictor of winter food availability, body condition, and subsequently spring departure time–all important attributes of an individual's winter performance and subsequent fitness. January through March total rainfall values were obtained from the Burnt Savannah meteorological station (Meteorological Service of Jamaica) located approximately 20 km east of the study site. American redstarts exhibit high winter site fidelity that rivals breeding philopatry (34).

Identifying Breeding Origins. We used the isotopic concentration of stable-hydrogen isotopes in tail feathers (3rd rectrix) as a proxy for breeding latitude. Tail feathers are known to be molted on the breeding grounds and reflect the isotopic composition of their breeding environment, which follows a latitudinal distribution. Isotopic signatures are also very repeatable within adult birds between years (mean SD = 5.05) indicative of high breeding philopatry. This estimate of breeding latitude allowed us to reliably quantify migration distance from Jamaica for each individual in units of (δH_f). Isotope analyses were conducted primarily at the Smithsonian Institution's Stable Isotope Mass Spectrometry Laboratory in Suitland, MD, USA.

To remove surface oils, tail feathers were washed in a 2:1 mixture of chloroform: methanol. Samples were equilibrated for 72 h at the lab where then a distal portion (length 3 to 5 mm) of each feather was collected, weighed to 350 ± 10 μg, and placed into a 4 × 6-mm silver capsule. Tissue samples were run using an elemental analyzer and an isotope ratio mass spectrometer integrated via a Conflo IV interface. We ran one in-house standard for every 5 to 8 unknowns to measure accuracy and precision. The nonexchangeable hydrogen (‰) was estimated via linear regression with in-house standards (Caribou Hoof Keratin, −196.90 ‰; Spectrum Keratin, −80.78 ‰; and Kudo Horn Keratin, −54.17 ‰).

Breeding origin of this population was estimated by assigning each individual to each 30 × 30 cell of a (δH_f) isoscape rescaled for redstarts (−25 ‰, 43). We used a normal probability density function to estimate the probability of a given redstart (δH_f) value originating from a given pixel. Each individual's probability surface was rescaled from 0 to 1 by dividing by the maximum probability and then clipping the surface to pixels with a probability >0.67 and assigning those pixels a value of 1. After repeating for each individual, we added all of the individual surfaces up to calculate a cumulative likelihood for the redstart population. For investigating the shift in breeding origin over time, we performed an inverse-variance weighted regression on mean annual δH_f over the past 30 y.

Although the use of stable isotope biogeochemistry to infer long-term changes in migratory connectivity is an important tool for ecologists (44), it can be prone to both short-term and long-term temporal variation that may influence our interpretations of these long-term shifts in connectivity. That said, short-term (annual/seasonal) variation in isotopic concentration do not appear to be reflected in animal tissues (45) and although long-term trends have been detected for some Global Network of Isotopes in Precipitation (GNIP) sites we found no such trends (*SI Appendix*, Table S4) within the seven GNIP sites situated broadly across the upper Great Lakes region (i.e., breeding region of our winter population). Within this context, stable hydrogen isotopes are an effective tool for monitoring long-term changes in connectivity.

Stable hydrogen isotopes provide great information on individual breeding latitudes but not longitudes. To further refine the breeding origins of this population and estimate the range of breeding longitudes occupied, we equipped 45 (9-2017, 36-2019) individuals with a 0.32-g light-level geolocator (Intigeo-W30Z11-DIP, Migrate Technologies LTD., Cambridge, UK) using a modified leg-loop harness made of stretch magic material (Pepperell Crafts, Pepperell, MA). Of those deployed, four of 9 were recovered in 2018, and 11 of 36 were recovered in 2020 (19 of 36 returned but 11 were recaptured) (12).

Stable hydrogen isotopes can provide information about an individual's breeding latitude, but not its longitude. To obtain a more precise determination of the breeding origins of this nonbreeding population and estimate the range of longitudes where they breed, we examined previously published data (12) from light-level geolocators that were placed on 16 individual birds from this population in 2017 and 2019. We analyzed the data using methods outlined in Lisovski et al. (2019) and the R package GeolocTools (46). We used the flightR package (47) to analyze the movement tracks and stationary distributions, but refer to Dossman et al. (2022) for more details.

We utilized both data sources detailed above to ultimately define the probable breeding region of our Jamaica redstart population. To accomplish this, we simulated breeding origins of 1,000 individuals where their respective latitude and longitudes were drawn randomly from realistic distributions estimated from the two data source independently. Latitudes were drawn from normal distribution with mean of 40.43° and SD of 2.86°. Longitudes were approximated by a normal distribution of mean −90.14° and SD of 2.78°. We then calculated 95% kernel density of these simulated data to ultimately delineate a probable breeding region. It's important to note that while the latitudinal estimates reflect an average breeding origin of the population of that past 30 y (1990 to 2019), the longitudinal estimates reflect the breeding origin of the population from the most recent 4 y (2016 to 2019). Therefore, it is possible that these recent assessment of breeding longitudinal may differ from the longitudinal origin of the breeding population from the early 90s.

Estimating Annual Survival. To estimate annual survival, we ran Cormack–Jolly–Seber (CJS) survival models with a fixed detection model that included habitat type (dry scrub forest vs. wet mangrove habitat) and sex as these were known previously to affect detection probability within this population (48). Model goodness-of-fit (GOF) was assessed using the R package R2Ucare and following recommendations therein (49). Overall, we determined that there was significant lack of fit ($\hat{c} = 1.80$, $X^2 = 82.61$, df = 46, $P = 0.001$), but that this was largely due to overdispersion within the male ($\hat{c} = 1.78$, $X^2 = 53.36$, df = 30, $P = 0.005$) rather than female datasets ($\hat{c} = 1.16$, $X^2 = 51.06$, df = 44, $P = 0.22$). Upon further inspection, overdispersion was largely attributed to transience within males ($X^2 = 39.21$, df = 16, $P = 0.001$). We found no strong evidence of trap heterogeneity for males ($X^2 = 7.26$, df = 6, $P = 0.297$). Accounting for transience, using a time-since-marking approach (50), resulted in a significantly better model fit ($\hat{c} = 1.26$, $X^2 = 38.01$, df = 30, $P = 0.15$).

We performed a two-step process when fitting survival models in order to limit the total number of model combinations that needed to be evaluated while also simplifying the model selection process. Our first step involved evaluating the best supporting base survival model that included the known factors that influence survival (*SI Appendix*, Table S2). This included the transience, habitat (dry scrub vs. wet mangrove), sex, and their respective two- and three-way interactions. We excluded any model that did not include a transience term given our GOF results. The top supporting model included both transience × sex and transience × habitat interactions was then used as the base model to evaluate the effects of winter rainfall and migration distance on survival while accounting for those factors. Finally, we evaluated the effect of winter rainfall and breeding latitude (δH_i) on survival while accounting for transience, sex, and habitat type. We evaluated all potential model combinations of sex, rain, and breeding latitude and their two-way and three-way interactions (*SI Appendix*, Table S3). Further, we also included a rain × habitat interaction given its demonstrated influence on survival in a previous study (48).

Winter rainfall was treated as a time-varying covariate. Only adults were included in the model and because adult breeding dispersal is relatively rare (25, 41, 51), we treated migration distance (δH_i) as an individual covariate. All CJS survival models were run in the R package *marked* (52). Confidence limits were calculated at the 95% level. All models were evaluated using Akaike's information criterion (53). All models <2 AIC units were treated as equally supported unless these models differed significantly in their number of parameters (54). To visualize how migration distance influenced survival following extreme drought and wet years, respectively we fixed rainfall to the lowest (<74 mm) and highest quartile (>272 mm) range over the 2002 to 2019 period.

Hierarchical BBS Abundance Model. To evaluate the hypotheis that tropical rainfall in Jamaica can impact the population dynamics of American redstarts on their breeding grounds, we relied on 30 y (1990 to 2019) of breeding bird abundance data collected as part of Breeding Bird Survey (BBS). These data were used in conjunction with rainfall and isotope data collected on our Jamaica nonbreeding population during that same time period. Data from 554 BBS routes included in this analysis were selected based on the likely breeding origins of this population (Fig. 1) detailed above.

We fit a hierarchical Poisson regression model using Markov chain Monte Carlo methods in Just Another Gibbs Sampler (JAGS) (55) implemented through R with package R2jags (56). Consistent with prior studies (14, 57, 58), we modelled each count $Y_{i,t}$ as a Poisson random variable with mean $\lambda_{i,t}$ defined as a log-linear relation to the predictor variables where *i* represents the route and *t* the year:

$$Y_{it} \sim Pois\left(\lambda_{i,t}\right),$$

$$\begin{aligned}\log\left(\lambda_{i,t}\right) = {} & \alpha + \beta_1 * t + \beta_2 * week_{i,t} + \beta_3 * \text{Breeding Rainfall}_{i,t} \\ & + \beta_4 * \text{Breeding Temperature}_{i,t} + \beta_5 * \text{Winter Rainfall}_t \\ & + \beta_6 * \text{Latitude}_i + \beta_7 * \text{Winter Rainfall}_t * \text{Latitude}_i + \text{Route}_i \\ & + \text{Observer}_{i,t}.\end{aligned}$$

The model includes estimates of log-linear population trends (β_1). β_2 represents the effect of week-of-year on abundance, β_3 accounts for breeding season (May – July) Total Rainfall, β_4 accounts for breeding season (May – July) average max temperature, and β_5 represents the effect of total winter rainfall (January – March) in Jamaica. β_6 accounts for the effect of Latitude on abundance and β_7 allows for a varying effect of winter rainfall by breeding latitude. We used uninformative normal priors with mean 0 and variance 10^2 for all beta parameters and diffuse uniform distributions for all variance parameters. To account for the nonindependence of observations on a given route, we included a random effect on the intercept for each route ($Route_i$) and observer ($Observer_{i,t}$), both with a Gaussian prior centered on 0. To compare the relative contributions of each factor on breeding bird abundance and to aid in computations, we centered and scaled all predictors so that values were in units of SD about the mean.

We generated 6,000 posterior distribution samples by running three chains of 25,000 iterations, discarding the first 5,000, and thinning the remaining by a factor of 10 for inference purposes. We assessed model convergence through the parameter histogram plots and Gelman–Rubin (R-hat) convergence diagnostics. We interpreted all effects by examining posterior mean and associated 95% credible intervals (CIs) for all β_i parameters.

Hierarchical Multiseason Occupancy Model. We modeled changes in occupancy probability with multiseason Bayesian hierarchical occupancy model implemented in the spOccupancy package in R (59). We utilized the BBS data from the abundance model above as occurrence data (presence/absence) by treating each of the 5 segments along a BBS route (pooled 10-stop summaries, 50 stops in total per route) as a replicate and converting all counts >1 as a detection and counts <1 as an absence. Conventional practice in occupancy modeling is to utilize temporal replicates to estimate detection probability. BBS routes are only sampled once per year and so occupancy models have been adapted to utilize spatial replicates (stops) as a substitute (60). However, it is important to note that this space-for-time substitution introduces potential spatial autocorrelation that may bias occupancy if not properly accounted for. We attempt to account for the correlation by including a route-level random effect on detection probability which would allow for stops within a route to be correlated. Ideally, modeling the spatial correlation directly would provide a more exact approach toward accounting for the survey structure (60). We modeled detection as a function the week of the year the route was run (centered and standardized) while accounting for random observer and route effects. Occupancy was modeled as a function of proportion of forest, a year trend (centered and standardized), and random route effects. The proportion of forest represents the area within 40km of a BBS route with forest cover >10%. These data were extracted from the Global Forest Change dataset (v1.6; (61)) using Google Earth Engine. We incorporated a AR(1) temporal covariance structure to formally account for its effect on occupancy dynamics. We fit the model with default noninformative on all β's and weakly informative priors on the AR(1) variance and correlation parameters following Doser et al. (59). We ran 3 chains for 10,000 iterations with a burn in of 2,000 iterations and thinning rate of 10 resulting in 2,400 posterior samples. We assessed model convergence through the parameter histogram plots and Gelman–Rubin (R-hat) convergence diagnostics. Significance of parameter estimates was evaluated by whether or not the 95% credible interval overlapped 0.

Data, Materials, and Software Availability. BBS and environmental data for the abundance and occupancy analysis are available on Dryad (https://doi.org/10.5061/dryad.280gb5msz). Previously published data were used for this work (In this study, we include data from 16 light-level geolocators (Fig. 1) that we have previously published on December 2022 in Ecology (https://doi.org/10.1002/ecy.3938). Here, we use these geolocator data, along side hundreds of isotope values, to refine the breeding origins of our winter population for subsequent analysis of the effects of winter rainfall on breeding bird abundance. These data represent a small portion of the total data used in this paper and supplement the primary data analysis. Further, these data are used entirely differently from the Ecology paper that focussed on migration rate using geolocators and radio transmitters. We have properly cited the Ecology paper in reference to the geolocator data. Geolocator data are available in ref. 12.

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