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Source: The Auk, 135(4) : 881-894

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-17-209.1

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The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 135, 2018, pp. 881–894
DOI: 10.1642/AUK-17-209.1

RESEARCH ARTICLE

Follow the rain? Environmental drivers of *Tyrannus* migration across the New World

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Submitted October 31, 2017; Accepted May 2, 2018; Published July 11, 2018

ABSTRACT

Predictable seasonal changes in resources are thought to drive the timing of annual animal migrations; however, we currently understand little about which environmental cues or resources are tracked by different migratory bird species across the planet. Understanding which environmental cues or resources birds track in multiple migratory systems is a prerequisite to developing generalizable conservation plans for migratory birds in a changing global environment. Within the New World, climatic differences experienced by Nearctic–Neotropical migratory (NNM; i.e. breed in North America and spend the nonbreeding period in the Neotropics) and Neotropical austral migratory (NAM; i.e. breed and spend the nonbreeding period wholly within South America) bird species suggest that their migratory strategies may be shaped by unique selective pressures. We used data gathered from individuals fitted with light-level geolocators to build species distribution models (SDMs) to test which environmental factors drive the migratory strategies of species in each system. To do so, we evaluated whether temperature, precipitation, and primary productivity (NDVI) were related to the seasonal distributions of an NNM (Eastern Kingbird [*Tyrannus tyrannus*]) and NAM species (Fork-tailed Flycatcher [*T. savana*]). Both Eastern Kingbird and Fork-tailed Flycatcher locations were positively correlated with high precipitation during their nonbreeding seasons. Eastern Kingbird locations were positively correlated with both NDVI and temperature during their breeding season and both pre- and post-breeding migrations. Fork-tailed Flycatcher locations were positively correlated with both temperature and precipitation during both migrations, but only temperature during the breeding season. The value of extending the application of geolocator data, such as in SDMs, is underscored by the finding that precipitation was such an important predictor of the nonbreeding distributions of both types of migrants, as it remains unclear how global climate change will affect wet–dry cycles in the tropics.

Keywords: migration, seasonality, species distribution model, geolocator, climate, Maxent

¿Siguiendo la lluvia? Controladores ambientales de la migración de *Tyrannus* a través del Nuevo Mundo

RESUMEN

Se piensa que los cambios estacionales de los recursos controlan el momento de la migración anual de los animales; sin embargo, es poco lo que entendemos actualmente sobre cuáles son las señales ambientales o los recursos que las diferentes especies de aves migratorias siguen a lo largo del planeta. Entender cuáles son las señales ambientales o los recursos que las aves siguen en múltiples sistemas migratorios es un prerrequisito para desarrollar planes de conservación generalizados para las aves migratorias en un ambiente global cambiante. En el Nuevo Mundo, las diferencias climáticas que viven las especies de aves migratorias neártico-neotropicales (MNN; i.e., se reproducen en América del Norte y pasan el período no reproductivo en el Neotrópico) y las migratorias australes del neotrópico (MAN; i.e., se reproducen y pasan el período no reproductivo de modo completo en América del Sur) sugieren que sus estrategias migratorias pueden estar moldeadas por las mismas presiones de selección. Usamos datos recopilados a partir de individuos provistos de geo-localizadores de nivel de luz para construir modelos de distribución de especies (MDEs) y así evaluar qué factores ambientales controlan las estrategias migratorias de las especies en cada sistema. Para hacer esto, evaluamos si la temperatura, la precipitación y la productividad primaria (NDVI) estuvieron relacionadas con las distribuciones estacionales de las especies MNN (*Tyrannus tyrannus*) y MAN (*T. savana*). Las

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ubicaciones de ambas especies estuvieron positivamente correlacionadas con una alta precipitación durante sus estaciones no reproductivas. Las ubicaciones de *T. tyrannus* estuvieron positivamente correlacionadas con la NDVI y la temperatura durante la estación reproductiva y con las migraciones pre- and post-reproductivas. Las ubicaciones de *T. savana* estuvieron positivamente correlacionadas con la temperatura y la precipitación durante ambas migraciones, pero solo con la temperatura durante la estación reproductiva. El valor de extender las aplicaciones de los datos de geolocalización, como en los MDEs, queda en evidencia por el hallazgo de que la precipitación fue un predictor tan importante de las distribuciones no reproductivas de ambos tipos de migración, que no está claro cómo el cambio climático global afectará los ciclos húmedos-secos en los trópicos.

Palabras clave: clima, estacionalidad, geo-localizador, Maxent, migración, modelo de distribución de especies

INTRODUCTION

Animals are thought to have evolved seasonal annual migrations to track spatiotemporal variation in resources that are ephemerally abundant in a predictable way (Dingle and Drake 2007, Milner-Gulland et al. 2011). The timing of seasonal migrations presumably matches optimum resource availability across a landscape to maximize fitness (Nathan et al. 2008, La Sorte et al. 2014), but studies quantifying resource optimality are rare (Bridge et al. 2016). We therefore lack a thorough understanding of the degree to which seasonal movements of animals are driven by the phenology (timing and sequence) of resource availability across space (Renfrew et al. 2013), and the degree of temporal flexibility in migratory movements with respect to seasonal resource abundance (Jenni and Kéry 2003). However, recent advances in animal tracking technology, including stable hydrogen isotopes (Studds et al. 2012), miniature light-level geolocators (Stutchbury et al. 2009, Bridge et al. 2011), and satellite transmitters (Robinson et al. 2010), offer an unprecedented ability to explore how individual animals track seasonal changes (e.g., Renfrew et al. 2013). This has been an especially fast-growing area of research in the study of bird migration, with evidence supporting major roles of seasonality in temperature (Schmaljohann et al. 2012), rainfall (Boyle 2008), and primary productivity (Renfrew et al. 2013, Bridge et al. 2016) in driving seasonal movements of individuals. Although highly correlated, the 3 main aspects of seasonality that have been identified as important predictors of the seasonal abundance of food used by migratory animals are the periodicity and amplitude of changes in temperature, rainfall, and primary productivity.

The general role of seasonality in driving the migrations of populations that breed, migrate, and spend the nonbreeding period across a variety of geographic and climatic contexts has yet to be evaluated; consequently, we lack a unified paradigm describing the ecological drivers of bird migration (Bairlein and Coppack 2006, Hedenström 2008, Nathan et al. 2008, Watts et al. 2018). Seasonal fluctuations in temperature covary with day length, which changes predictably throughout the year at any given latitude, with the seasonal amplitude of changes in temperature increasing with latitude. Rainfall in terrestrial biomes is less predictable than temperature because, at a local scale, patterns of rainfall are driven by temperature (Santer et al. 2007, Willett et al. 2007), geographical location and topography (Ineson and Scaife 2009, Kenyon and Hegerl 2010), and the abundance of greenhouse gases (Allen and Ingram 2002, Lambert and Allen 2009, Polson et al. 2013). The seasonality of primary productivity is even less predictable, because it can be affected not only by topography or ecoregion (Forzieri et al. 2014), but also by stochastic, abiotic factors such as droughts (e.g., Hoerling et al. 2014), El Niño–La Niña cycles (Goetz et al. 2000, Abdi et al. 2016) and by complex species-specific biotic factors such as symbioses with pollinators (Mosquin 1971) or the synchrony of fruiting (van Schaik et al. 1993). Thus, if seasonality is important in the evolution of optimal annual routines by migratory birds, it is likely that birds track aspects of the environment that vary in the most reliable ways for a given location and time of year.

The 2 largest bird migration systems in the New World, in terms of numbers of species, are Nearctic–Neotropical and Neotropical austral bird migration systems (Faaborg et al. 2010). Nearctic–Neotropical migrants (hereafter, NNMs) breed in North America and migrate south to spend the nonbreeding period in the Neotropics (Faaborg et al. 2010). Conversely, Neotropical austral migrants (hereafter, NAMs) breed in southern South America and migrate north to spend the nonbreeding period closer to the equator, thus spending their entire annual cycle within South America (Chesser 1994, Cueto and Jahn 2008).

For several reasons, birds in these 2 migration systems may experience unique climates. Broadly, as the oceans encompass a greater proportion of the Southern compared with the Northern Hemisphere, terrestrial ecosystems in the south may be better buffered against temperature extremes and therefore may experience an overall milder climate than northern temperate terrestrial systems (Hayes et al. 1994, Yom-Tov et al. 1994, Paruelo et al. 1995, Dingle 2008). Thus, the amplitude and periodicity of temperature as a reliable seasonal cue is likely to be smaller in South vs. North America. To add to this, food resources (i.e. arthropods) important for insectivorous migratory birds in North America emerge with seasonal changes in temperature (Both et al. 2006, Mazerolle and Hobson 2007, Tulp and Schekkerman 2008), whereas food

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resources for such birds in South America are likely to be driven by seasonality in rainfall (Pinheiro et al. 2002, Jahn et al. 2010b, Mendoza et al. 2017).

While there is some research linking seasonal locations of NNMs with primary productivity (e.g., geese species track spring growth of plants during prebreeding migration: Drent et al. 2007; Bobolinks [*Dolichonyx oryzivorus*] track primary productivity during the nonbreeding period: Renfrew et al. 2013; Painted Buntings [*Passerina ciris*] optimize whole annum exposure to primary productivity: Bridge et al. 2016), there have been no assessments of which aspects of the environment NAMs may be tracking (but see Jahn et al. 2010a, Guaraldo et al. 2016). Although climatic differences experienced by birds in these 2 migration systems suggest that different environmental selective pressures may shape their life history strategies, we have yet to test how birds in different New World migratory systems track seasonally variable cues or resources throughout their annual cycles.

Here, we provide the first assessment of the role of extrinsic factors (e.g., seasonality experienced by a migratory bird) in explaining the locations of individual NNMs vs. NAMs throughout their annual cycles (i.e. annual life history stages). We used species distribution models (SDMs) to test whether aspects of seasonality (temperature, rainfall, and/or primary productivity measured using the Normalized Difference Vegetation Index [NDVI]) best explained the locations of an NNM, the Eastern Kingbird (*Tyrannus tyrannus*), and an NAM, the Fork-tailed Flycatcher (*T. savana*), during 4 major life history stages: breeding, postbreeding migration, nonbreeding, and prebreeding migration. Eastern Kingbirds breed in North America and spend the nonbreeding period in South America (Murphy and Pyle 2018), whereas the nominate subspecies of Fork-tailed Flycatcher resides primarily in South America throughout the annual cycle, breeding from central South America to central Argentina and spending the nonbreeding period in northern South America (Jahn et al. 2013b). Both species occupy savanna habitat, perch in the open, are similar in size, and forage by aerial hawking and upward sallies in pursuit of their primary prey, flying insects (Fitzpatrick et al. 2004). Both are also known to forage on fruit during the nonbreeding period (Zimmer 1938, Morton 1971, Jahn and Tuero 2013).

Environmental variables that are correlated with species occupancy are expected to be reflected in species' realized niches (Elith et al. 2006), and comparisons of SDMs have been used to better understand the ecological basis of speciation or barriers to hybridization in closely related species (Cicero 2004, Graham et al. 2004). We compared SDMs for Eastern Kingbirds and Fork-tailed Flycatchers to better understand the ecological underpinnings of migration strategies within North vs. South American breeding birds. We predicted that primary productivity would be the best estimator of locations of Eastern Kingbirds during the summer breeding months, but that rainfall would best estimate locations during their nonbreeding season in South America, since food resources for birds are likely driven by seasonality in rainfall there (Pinheiro et al. 2002, Jahn et al. 2010b, Mendoza et al. 2017). Because temperature has been strongly linked with the timing of pre- and post-breeding migration in migrant birds that breed in the Northern Hemisphere (Jenni and Kéry 2003), we predicted that temperature would be the best predictor of locations of Eastern Kingbirds during both migrations. We predicted that rainfall would be the best estimator of locations of Fork-tailed Flycatchers during all 4 annual life history stages because they reside in South America throughout their annual cycle (Jahn et al. 2013b).

METHODS

Capture and Deployment of Light-level Geolocators

We captured Eastern Kingbirds and Fork-tailed Flycatchers during their respective breeding seasons (Eastern Kingbirds: May to July in Nebraska, Oklahoma, and Oregon, USA [Murphy and Pyle 2018]; Fork-tailed Flycatchers: September to December in Brazil [Marini et al. 2009] and October to January in Argentina [Jahn et al. 2014]). Three Eastern Kingbirds were tracked in 2009–2010, 6 in 2010–2011 (raw geolocator data from these birds from Nebraska has also been used by Jahn et al. 2013a) and 3 in 2011–2012 (raw geolocator data from 1 of these individuals has also been used by Jahn et al. 2013a; Table 1). One Eastern Kingbird was tracked across 2 yr; thus, the 12 geolocator tracks that we analyzed came from 11 individual Eastern Kingbirds. Two Fork-tailed Flycatchers were tracked in 2009–2010, 9 in 2010–2011 (raw geolocator data from 6 of these individuals has also been used by Jahn et al. 2013b), and 8 in 2011–2012. Three Fork-tailed Flycatchers were tracked across 2 yr, thus the 19 geolocator tracks that we analyzed came from 16 individual Fork-tailed Flycatchers (Table 1).

Light-level geolocators were attached to birds using a backpack-style harness (Rappole and Tipton 1991) made of spun Kevlar filament (500 decitex; Saunders Thread, Gastonia, North Carolina, USA; Jahn et al. 2013a). The mass of each unit with the harness was $\sim$1.2 g and $<$5% of the body mass of each individual (see Table 1 for a comprehensive list of the geolocator models deployed).

Analysis of Geolocator Data

We analyzed geolocator data to determine the dates and locations of stops made by each individual during the annual cycle. For every individual, we used the recorded light intensity from all geolocators at the specific deployment site to calibrate geolocator data by calculating

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TABLE 1. Geolocators recovered from individual *Tyrannus* species at different study sites, from which stopped locations were used to inform species distribution models (SDMs). Distributions of stopped locations were used to test which environmental factors were correlated with the distributions of a Nearctic–Neotropical migrant (NNM; the Eastern Kingbird), which bred in North America and migrated south to spend the nonbreeding period in the Neotropics, and a Neotropical austral migrant (NAM; the Fork-tailed Flycatcher), which bred in southern South America and migrated north during the nonbreeding period, spending its entire life cycle in South America. The types of geolocators deployed included: BAS (Mk 20), weighing 0.9 g and manufactured by the British Antarctic Survey (Wareham, Dorset, UK); BAS (Mk 10S), 1.2 g by the British Antarctic Survey; BAS (Mk 12S), 0.9 g by the British Antarctic Survey; and Eli Bridge, weighing 0.7 g and developed by researchers at the University of Oklahoma (Norman, Oklahoma, USA) and Cornell University (Ithaca, New York, USA).

Type of migrant	Species	Study site (latitude, longitude)	Types of units deployed	Dates geolocators were deployed (sample size)
NNM	Eastern Kingbird	Oklahoma, USA (34.6°, −98.4°)	BAS (Mk 20)	June 2011 to May 2012 (2)
		Nebraska, USA (40.8°, −98.4°)	BAS (Mk 20)	July 2010 to June 2011 (5), July 2010 to July 2012 (1)
		Oregon, USA (42.9°, −118.8°)	BAS (Mk 20)	July 2009 to August 2010 (1), July 2009 to July 2010 (2)
				(Total = 11)
NAM	Fork-tailed Flycatcher	Brasilia, Brazil (−15.5°, −47.6°)	Eli Bridge	November 2010 to November 2012 (1)
		Buenos Aires, Argentina (−34.1°, −57.4°)	BAS (Mk 10S and Mk 12S), Eli Bridge	December 2009 to December 2010 (2), February 2010 to December 2011 (2), December 2010 to December 2011 (1), December 2010 to December 2012 (2), December 2010 to November 2011 (2), January 2011 to November 2011 (1), October 2011 to December 2012 (1), November 2011 to December 2012 (2), December 2011 to December 2012 (1), December 2011 to November 2012 (1)
				(Total = 16)

sun zenith angles and measuring error. As geolocators were deployed on individuals at their nest sites, while they were incubating eggs or caring for nestlings, we assumed that individuals remained at the deployment site for at least 10 days after capture, and used the latitude and longitude of these sites to generate a calibration curve of light intensity as a function of zenith angles using astronomical functions within the R package SGAT (Wotherspoon et al. 2013). From data recorded at the deployment sites, we estimated geolocation error in longitude to be an average (± SE) of 52.1 ± 25.4 km and error in latitude to be an average of 85.1 ± 57.4 km for Eastern Kingbirds. For Fork-tailed Flycatchers, the average (± SE) error in longitude was 76.5 ± 14.77 km, and the average error in latitude was 101.3 ± 28.2 km. The derived zenith angle varied between individuals and ranged from −7.16 to 0.21. Daily positions for all geolocator types were estimated using the GeoLight package (Lisovski and Hahn 2012) in program R 3.4.3 (R Core Team 2017). Since the variation in elevation angle of the sun at the breeding grounds is low, and these species occupy open habitats throughout their annual cycle, we did not expect location accuracy to change throughout the year. We omitted location estimates within 2 weeks (14 days) of the fall and spring equinoxes for all geolocators (see Renfrew et al. 2013), and applied a local regression (loess) filter to remove outlier location data from all geolocation tracks (Cormier et al. 2013). Since open-habitat species produce extremely 'clean' datasets for identifying sunrise and sunset times compared with avian species that occupy other habitat types, aberrant location estimates were easily identified and deleted (Phillips et al. 2004). R code and further explanation of light-level data analysis are given in Supplemental Material Appendix A.

Environmental Datasets

We obtained daily temperature and precipitation data for the Americas from July 2009 through October 2012 from the National Centers for Environmental Prediction (NCEP) database (Kalnay et al. 1996). We obtained Normalized Difference Vegetation Index (NDVI) data from NASA's MODIS dataset (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD_NDVI_16&year=2009). NDVI is a satellite-derived 'greenness' index that is used as a proxy for primary productivity or food availability (reviewed by Pettorelli et al. 2005) and has been used to assess movement decisions of birds in South America, the Middle East, and northern Europe (Tøttrup et al. 2008, Renfrew et al. 2013).

Prior to analysis, we calibrated the time period and spatial resolution of these 3 environmental datasets. NDVI is measured remotely via satellite and captures a single file with global reflectance data every 16 days at a spatial resolution of 1.0° × 1.0°. Temperature and precipitation

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rasters obtained from the NCEP database have a 2.5° × 2.5° spatial resolution. To combine these datasets for our analyses, the daily high temperature and cumulative rainfall for each day were calculated and then averaged for each 16-day period defined by the NDVI dataset. Numerical control files were converted from the NCEP database to GeoTiff files using NASA SeaDas software (version 7.3.2) and then stacked, and rasters were made of temperature and rainfall data using the rgdal (Bivand et al. 2016) and raster (Hijmans 2016) packages in R 3.4.3 (R Core Team 2017; Supplemental Material Appendix B). Using the projectRaster function in the raster library in R, the spatial extent of NDVI rasters was set to meet the pixel size of temperature and rainfall rasters (Supplemental Material Appendix B).

Statistical Analyses and Spatial Models

We built SDMs using 3 environmental variables (temperature, precipitation, and NDVI) for both bird species for each 16-day time period during the time that geolocators collected data. This totaled 59 SDMs for Eastern Kingbirds (from July 12, 2009, to May 9, 2012, was 1,033 days, which, after subtracting equinox periods and dividing by 16-day time periods, left 59 time periods for SDMs), and 60 SDMs for Fork-tailed Flycatchers (from December 19, 2009, to November 1, 2012, was 1,049 days, which, after subtracting equinox periods and dividing by 16-day time periods, left 60 time periods for SDMs). To test whether the environmental variables estimated the distributions of the locations of migrants throughout the annual cycle, we used a maximum entropy (MaxEnt) modeling approach. Maxent software uses presence-only data to build ecological niche models to quantify the probability of the presence of a species in a region (Phillips et al. 2006, Phillips and Dudík 2008). We assigned each 16-day time period to the most appropriate life history stage (i.e. breeding, postbreeding migration, nonbreeding, and prebreeding migration) following species accounts for each species (Pyle 1997, Marini et al. 2009, Jahn and Tuero 2013, Jahn et al. 2014). We used Maxent to estimate species distribution models (SDMs) during each annual life history stage from 2009 to 2012.

To assess the performance of the 3 environmental variables in describing the distributions of both species, we generated Maxent models by training each model with location data from individuals fitted with geolocators. To do this, we used the geolocator data as a presence-only dataset, and identified single stationary locations for every individual during each time period. If multiple locations were estimated for any individual during a time period, we used the location where individuals occupied the largest number of days during that time period in our model. We then tested the SDMs against a second independent presence-only dataset gathered from eBird (https://ebird.org/). Date and location data were downloaded from the eBird website for Eastern Kingbirds and Fork-tailed Flycatchers from July, 2009, through October, 2012. During each time period for Eastern Kingbirds (59) and Fork-tailed Flycatchers (60), we randomly selected 10 locations. We selected 10 locations per time period from eBird because this was a standard number of sightings that could be replicated across each time period for both species to create a balanced test dataset. For Eastern Kingbirds, the fewest records occurred during the nonbreeding seasons (October–March), and we allowed eBird records to be drawn from anywhere in the Americas. Fork-tailed Flycatchers had the fewest eBird records during the months of May and June across all years. As Fork-tailed Flycatchers have multiple nonmigratory subspecies that are not distinguished in the eBird dataset, we placed restrictions on the selection of eBird records to reduce error in our tests of SDMs built from geolocator data of the migratory subspecies. We restricted eBird records for Fork-tailed Flycatchers to South America for all seasons, and limited records to south of the Amazon Basin during the breeding season, and north of the Amazon Basin during the nonbreeding season.

We generated SDMs with the training (geolocator) and test (eBird) data using Maxent 3.3.3k (http://biodiversityinformatics.amnh.org/open_source/maxent/). We trained each SDM using geolocator data against a random set of 10,000 background points constrained to be located within the potential range of each taxa (the entirety of the Americas for Eastern Kingbirds, and solely South America for the subspecies of Fork-tailed Flycatcher that we studied). We attempted to avoid overfitting by drawing geolocator data from multiple breeding populations (limiting sampling bias), training SDMs using regularization via the default settings of the Maxent program (Phillips and Dudík 2008), using a second independent test dataset (eBird data), and using a geographic area appropriate to each species. However, our approach to assessing the role of seasonality in predicting locations of long-distance migrants is expected to be overfitted due to the large number of background points (Phillips and Dudík 2008) and large spatial extent that, by design, was not meant to impose spatial limitations from biotic interactions or limits to dispersal (Anderson and Raza 2010). Models were considered to have performed well if AUC (area under the curve) values were above the 0.5 threshold, indicating a strong discrimination between the environment (e.g., temperature, precipitation, NDVI) where individuals were present vs. other potential locations (Elith et al. 2011). Significant drops in AUC values from training to test datasets would indicate model overfitting, and this was monitored.

The importance of environmental variables to determining distributions during each time period was assessed

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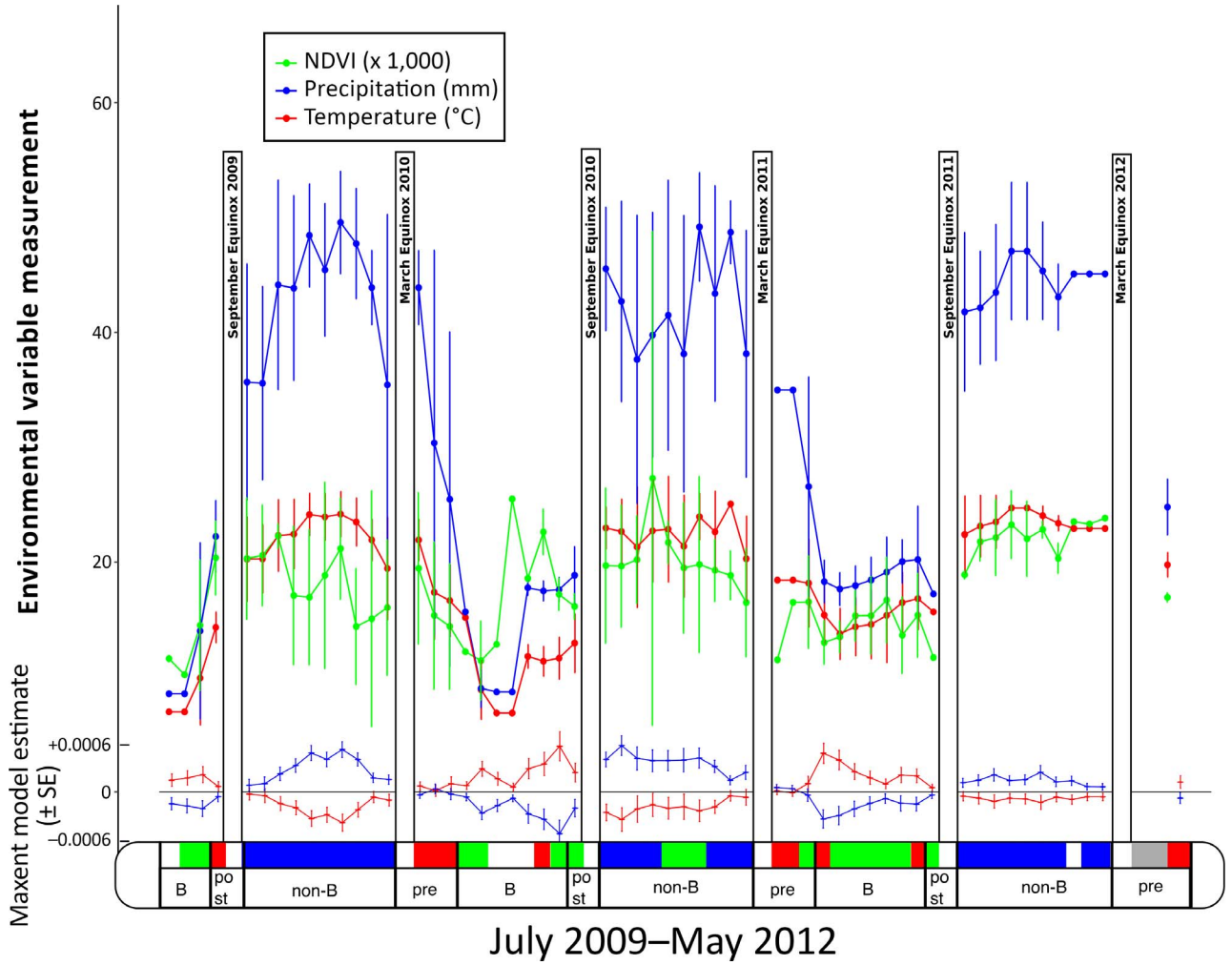


FIGURE 1. Environmental variables experienced by Eastern Kingbirds fitted with geolocators (mean ± SE). NDVI is a satellite-derived 'greenness' index that is used as a proxy for primary productivity. The environmental variables that were significant for defining the seasonal ranges of individual Eastern Kingbirds fitted with geolocators are identified by colored bars along the *x*-axis; colors match the measurement values displayed in the figure. White bars along the *x*-axis indicate that none of the environmental variables predicted bird locations, and gray bars indicate that not enough location data were available to build species distribution models (SDMs). The letters along the *x*-axis indicate seasons as follows: B = 'breeding,' post = 'postbreeding migration,' non-B = 'nonbreeding,' and pre = 'prebreeding migration.'

using percent contribution and permutation importance using the Maxent software. For each model, the program identified the proportional contribution of each environmental layer by detecting changes in model gain by modifying coefficients in each layer (Phillips et al. 2006). The final percent contributions were assigned according to changes in model gain when each layer was modified. Permutation importance is a second assessment of importance calculated in Maxent by randomly permuting the values within each environmental dataset of both the training and background points. Each model was reevaluated based on the permuted environmental data and the change in AUC was calculated. Large changes in AUC indicated that the variable had high importance in the SDM. Permutation analyses distinguish the influence of environmental variables from one another, allowing for the inclusion of relevant variables regardless of correlation between them. However, all environmental variables were checked for multicollinearity, and correlated pairs ($r \geq 0.7$) were identified using ENMTools (www.enmtools.com; Fielding and Haworth 1995, Warren et al. 2008; Supplemental Material Appendix C).

RESULTS

Maxent models for the NNM (Eastern Kingbird) performed well in 52 of the 59 time periods (Figure 1; Supplemental Material Appendix D). Most of the contributing models (i.e.

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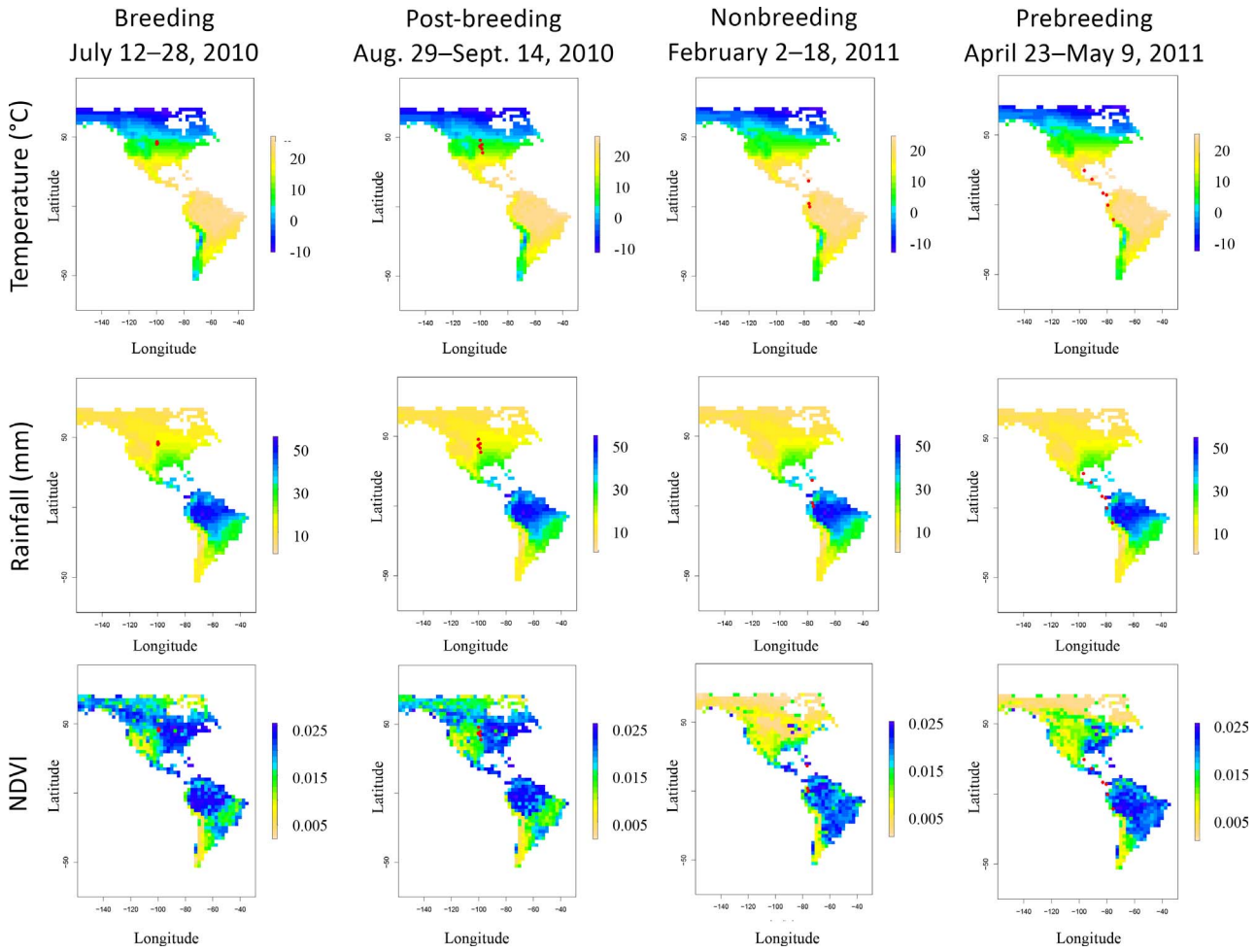


FIGURE 2. An example of seasonal locations of Eastern Kingbirds ($n = 6$) on the environmental landscape during 2010–2011. Locations of individual birds are represented by red dots. Time periods displayed are: the breeding season (July 12–July 28, 2010); postbreeding migration (August 29–September 14, 2010); the nonbreeding season (February 2–February 18, 2011); and prebreeding migration (April 23–May 9, 2011). See Figure 1 for NDVI definition.

those with AUC values >0.50) had AUC values above 0.850 (range: 0.606–0.998; test AUC values never dropped more than 0.10 below training AUC values), with the lowest values mainly found during prebreeding migration (Supplemental Material Appendix D). Positions of Eastern Kingbirds were positively correlated with NDVI (10/17 time periods) or temperature (3/17 time periods) during the breeding season (Figures 1 and 2, Supplemental Material Appendix D). The influence of NDVI in Maxent models was highly variable and irregular, compared with that of temperature and precipitation (Supplemental Material Figure S5A), and thus was omitted from Figure 1. Positions of Eastern Kingbirds were primarily correlated with high rainfall during the nonbreeding season (26/30 time periods) in South America, except when they were positively correlated with NDVI (3/10 time periods during the 2010–2011 nonbreeding season; Figures 1 and 2, Supplemental Material Appendix D). Eastern Kingbird positions were positively correlated with either temperature (6/9 time periods) or NDVI (1/9 time periods) during prebreeding migration, when enough data were available (Figures 1 and 2, Supplemental Material Appendix D). Their positions were positively correlated with NDVI (2/3 time periods) or temperature (1/3 time periods) during post-breeding migration (Figures 1 and 2, Supplemental Material Appendix D).

Maxent models for the NAM (Fork-tailed Flycatcher) performed well in 49 of 60 time periods (Figure 3, Supplemental Material Appendix D). Most of the contributing models (i.e. those with AUC values >0.50) had AUC values above 0.850 (range: 0.717–0.999; test AUC values did not drop more than 0.15 below training AUC values), with the lowest values mainly found during the breeding season (Supplemental Material Appendix D). When considering significant contributions from environmental variables during time periods with high

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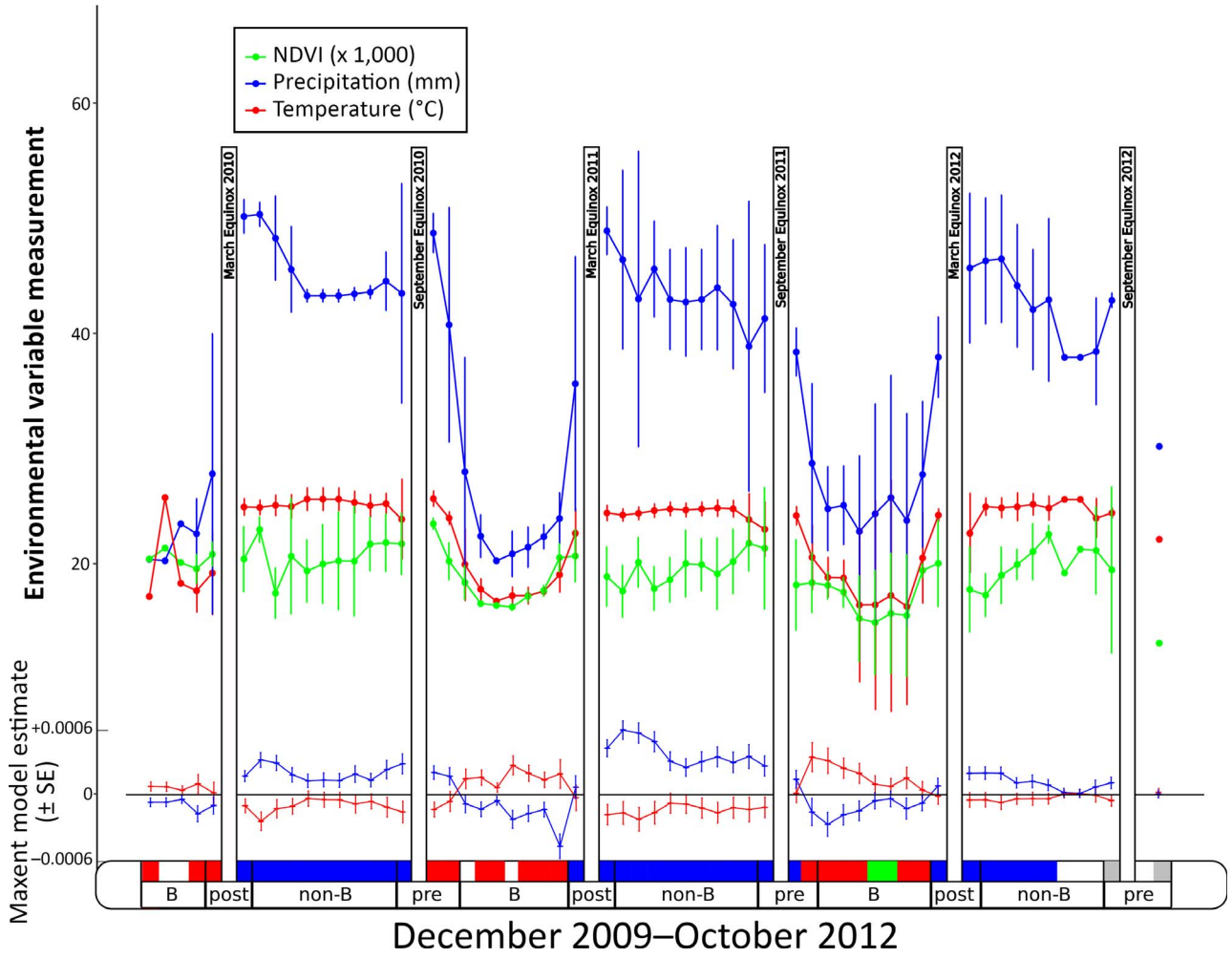


FIGURE 3. Environmental variables experienced by Fork-tailed Flycatchers fitted with geolocators (mean ± SE). The environmental variables that were significant for defining the seasonal ranges of individual Fork-tailed Flycatchers fitted with geolocators are identified by colored bars along the *x*-axis; colors match the measurement values displayed in the figure. White bars along the *x*-axis indicate that none of the environmental variables predicted bird locations, and gray bars indicate that not enough location data were available to build species distribution models (SDMs). The letters along the *x*-axis indicate seasons as follows: B = 'breeding,' post = 'postbreeding migration,' non-B = 'nonbreeding,' and pre = 'prebreeding migration.' See Figure 1 for NDVI definition.

AUC values, we found that Fork-tailed Flycatcher positions were positively correlated with temperature during the breeding season (12/18 time periods), except in the 2011–2012 breeding season, when locations were positively correlated with NDVI (2/7 time periods; Figures 3 and 4, Supplemental Material Appendix D). The influence of NDVI in Maxent models for Fork-tailed Flycatchers was highly variable and irregular, compared with that of temperature and precipitation (Supplemental Material Figure S5B), and thus was omitted from Figure 3. Fork-tailed Flycatcher positions were positively correlated with high rainfall during each nonbreeding period (during 23/27 time periods; Figures 3 and 4, Supplemental Material Appendix D). The distributions of Fork-tailed Flycatchers during both migrations seemed to bookend the environmental variable with which it was correlated during either the breeding or nonbreeding period (Figure 3). During postbreeding migration, their positions were positively correlated with temperature during 1/6 time periods and with precipitation during 5/6 time periods (Figure 3, Supplemental Material Appendix D). During prebreeding migration, their positions were positively correlated with temperature during 3/6 time periods and with precipitation during 3/6 time periods (Figure 3, Supplemental Material Appendix 4).

We seldom found the positions of either species to be highly correlated with more than one variable during any time period (Supplemental Material Appendix D).

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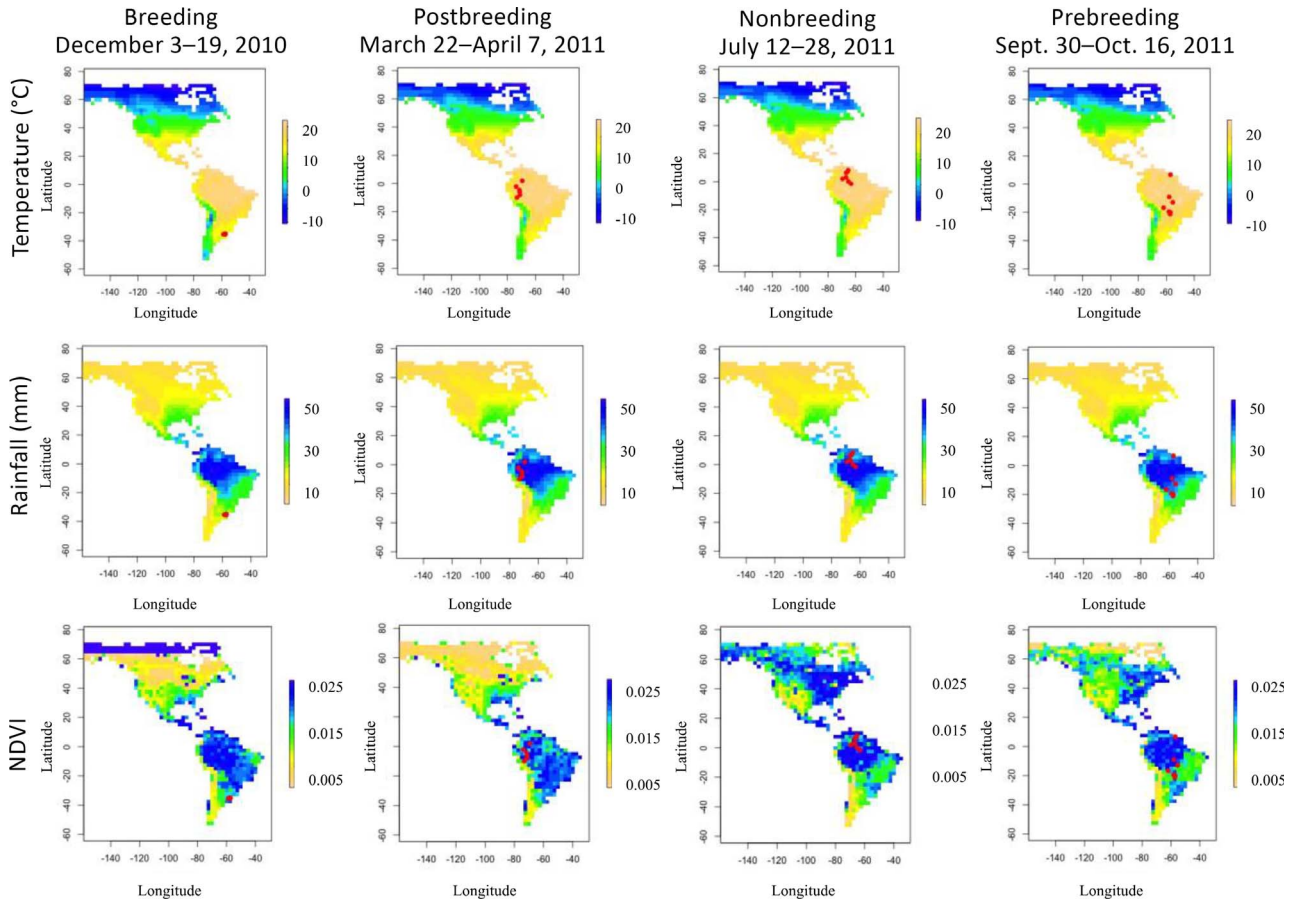


FIGURE 4. An example of seasonal locations of Fork-tailed Flycatchers ($n = 7$) on the environmental landscape during 2010–2011. Locations of individual birds are represented by red dots. Time periods displayed are: the breeding season (December 3–December 19, 2010); postbreeding migration (March 22–April 7, 2011); the nonbreeding season (July 12–July 28, 2011); and prebreeding migration (September 30–October 16, 2011). See Figure 1 for NDVI definition.

DISCUSSION

We found that the locations of a Nearctic-Neotropical migrant were correlated with a variety of season-specific climatic variables, while those of a Neotropical austral migrant were primarily correlated with temperature during the breeding season and with high rainfall during the nonbreeding season. Despite spatiotemporal differences between these 2 life-history strategies, we also found similarities, such as the nonbreeding locations of both species being correlated with high rainfall.

Although widely separated by space and time of year, the positions of both Eastern Kingbirds and Fork-tailed Flycatchers were positively correlated with temperature while on the breeding grounds. However, Eastern Kingbird locations were positively correlated more often with NDVI than with temperature while on the breeding grounds, signaling strong selection for matching the timing of reproduction with seasonally abundant resources in the Northern Hemisphere. Our finding that the positions of Eastern Kingbirds were positively correlated with NDVI during prebreeding migration was weak (only 1/9 time periods) and was likely an artifact of our approach, because individuals could have been moving large distances not captured by the 16-day time period. While temperature is thought to be positively correlated with the spring onset of insect activity, increased NDVI as well as rates of NDVI in spring may also be reasonable proxies indicating seasonal resource abundance (Hahn et al. 2016). In the Neotropics, native arthropods are typically abundant during the wet season, but some research suggests that certain arthropod groups do not decline during the tropical dry season (Pinheiro et al. 2002). New research is demonstrating that some herbivorous insects, including some exotic species (Coutinho-Silva et al. 2017), are in greater abundance during the dry season (Silva et al. 2017), when Fork-tailed Flycatchers are breeding. That the positions of Fork-tailed Flycatchers were predominantly correlated with temperature while breeding, and were neither positively nor negatively correlated with rainfall, underscores our poor

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understanding of migratory strategies in the understudied Neotropical austral migrant system (Jahn et al. 2004), and demonstrates that a more complex relationship with seasonality and resource availability may exist (e.g., Bridge et al. 2016).

Our results support the idea that, for closely related migratory species or those of the same dietary guild, tracking seasonally abundant resources throughout the year may be more season- and location-specific, rather than species-specific. As predicted, the positions of both species were positively correlated with rainfall during their nonbreeding seasons in South America, where temperature is less variable. Eastern Kingbirds are known to be seasonally frugivorous while on the nonbreeding grounds in South America during the wet season months of October through February (Zimmer 1938, Morton 1971, Jahn et al. 2013a), further suggesting a reliance on seasonally abundant resources throughout the annual cycle.

In addition to occupancy being positively correlated with temperature during parts of the breeding seasons, the positions of both species were also correlated with temperature during at least some parts of their pre- and post-breeding migrations, perhaps supporting the idea that migrants may be able to adjust their migrations in response to global climate change (Dunn and Winkler 1999, Hüppop and Hüppop 2003, Marra et al. 2005). However, one study of an NNM (Wood Thrush [*Hylocichla mustelina*]) that tracked individuals over multiple years showed flexibility in route, but not in timing, of migration (Stanley et al. 2012). Our results during migration lack such detail, as we used the longest stops during each 16-day period defined by the NDVI dataset. Thus, assessments of the timing of migration with respect to changes in climate are more appropriate using environmental data gathered at finer temporal scales than presented here.

Extending the application of fine-scale and full annual cycle tracking data, such as geolocator data or satellite data, to SDMs can improve our understanding of the temporal dynamics of climatic niches for migratory birds (Eyres et al. 2017, Thorup et al. 2017, Williams et al. 2017). Comparing the results of such applications with primary productivity data at smaller temporal scales (such as LiDAR data) may reveal more nuanced aspects of the timing of movements and stopovers during migration and allow more detailed tests of the flexibility of migrants in their responses to global climate change. This is especially relevant when considering our finding that precipitation was a significant predictor of occupancy during the nonbreeding season in South America. It is important to understand how migrants track wet–dry cycles during the nonbreeding season because, while there is agreement amongst climate models for projected changes in temperature, it remains unclear how changes in the amplitude or distribution of precipitation will affect resource availability (Tulp and Schekkerman 2008). While our study united full annual cycle tracking data with physical environmental variables characteristic in defining seasonality, we did not take into account other factors that contribute to a species' realized niche (such as competition or predation), or its fundamental niche (such as specific habitat requirements). Broadening the scope of SDMs to include biotic interactions could improve the impact of SDMs on conservation by distinguishing the realized from the fundamental niche (Phillips and Dudík 2008). This is of particular importance for species that practice wintering itinerancy, and for which we have little information on the drivers of nonbreeding movements (Thorup et al. 2017).

Models of optimal annual routines for migratory birds may be improved for some species with the inclusion of seasonal dynamics in climatic niches. If seasonality in arthropod abundance is driven in large part by the highly variable wet–dry cycle in South America (Wolda 1978, Jahn et al. 2010b, Morán-Tejeda et al. 2016, Osman and Vera 2017), migratory species that spend all or part of the year in South America may have evolved flexibility in the timing of their nonbreeding movements. Our results showed that the positions of Fork-tailed Flycatchers were positively correlated with rainfall throughout much of their annual cycle, including during both pre- and post-breeding migration. However, long-term studies in South America, and in particular in the Neotropical austral migration system, are necessary to test whether the timing of migration in NAMs matches that of variable wet–dry cycles, as has been done to test whether migratory birds breeding at northern temperate latitudes time their migration with increasing temperatures (e.g., Jenni and Kéry 2003). When considering species that may have evolved flexibility in their annual behavior, and that may have switched climatic niches intra-annually, full-cycle models testing optimization of resource acquisition may be more complicated than optimizing a single environmental variable (such as primary productivity; e.g., Painted Buntings: Bridge et al. 2016; Common Cuckoos (*Cuculus canorus*), Red-backed Shrikes (*Lanius collurio*), and Thrush Nightingales (*Luscinia luscinia*): Thorup et al. 2017).

Our findings support the idea that aspects of seasonality important to migrants are context-dependent and vary across continents and hemispheres. An important step moving forward will be to test the flexibility of routines of migratory birds in different migratory systems to predict and plan for differing responses by migratory bird species to global climate change. Developing seasonal SDMs for a variety of bird species tracked with geolocators and other tracking technologies will allow greater precision in our understanding of the movements of birds that migrate in

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different regions in relation to different seasonal cues or seasonal abundance of resources. In turn, this will better equip us to test whether and how the seasonal annual cycles of birds in different migratory systems will be affected under future global climate change scenarios (see Yesson and Culham 2006, Kharouba et al. 2009, Yates et al. 2010).

ACKNOWLEDGMENTS

We thank Dr. Emily McKinnon for organizing this special issue, and Dr. Mikkel Willemoes, Dr. Jorge Vega, and 2 anonymous reviewers for providing important feedback that led to the final version of this manuscript. We also thank the members of the University of Missouri's School of Natural Resources Writing Workshop for reviewing earlier versions of this manuscript.

Funding statement: This study was funded by the National Geographic Society (grant numbers 8444-08 and 8953-11), a National Science Foundation International Research Fellowship to A.E.J. (IRFP-0965213), a National Science Foundation grant to M.T.M. (IOB-0639370), the Gatorade Fund–University of Florida, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Cameron University's Dr. Bobby Gene Vowell Endowed Lectureship in the Physical and Biological Sciences, and the Fundação de Amparo à Pesquisa do Estado de São Paulo (#2012/17225-2). None of our funders had any input into the content of the manuscript, nor did they require their approval of the manuscript prior to submission or publication.

Ethics statement: This research was undertaken in compliance with required Institutional Animal Care and Use Committee (IACUC) regulations and research permissions in each country.

Author contributions: M.P.M. and A.E.J. conceived the idea, design, experiment (supervised research, formulated question or hypothesis); all authors performed the experiments (collected data, conducted the research) and wrote the paper; M.P.M. developed or designed the methods; M.P.M. and E.D.H. analyzed the data; and A.E.J., M.T.M., V.R.C., and D.T. contributed substantial materials, resources, or funding.

Data deposits: All geolocator data can be found at Movebank (https://www.movebank.org/), ID 467033356.

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