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LONG-DISTANCE BIRD MIGRATION WITHIN SOUTH AMERICA REVEALED BY LIGHT-LEVEL GEOLOCATORS

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Abstract.—Little is known about the timing of migration, migration routes, and migratory connectivity of most of the >230 species of birds that breed at south temperate latitudes of South America and then migrate toward the tropics to overwinter. We used light-level geolocators to track the migration of 3 male and 3 female Fork-tailed Flycatchers (*Tyrannus savana*) captured on their breeding territories in Argentina. All birds initiated fall migration between late January and late February, and migrated 45 to 66 km day^{-1} in a northwesterly direction through central South America to either one or two wintering areas. Five individuals first spent several weeks (in April and May) in western Amazonia (mainly Peru, northwestern Brazil, and southern Colombia) before moving east to spend the rest of the non-breeding season in central Venezuela and northern Brazil. One individual occupied primarily one wintering area in eastern Colombia, northwestern Brazil, and southwestern Venezuela. Fall migration took approximately 7–12 weeks to complete and covered a distance of 2,888–4,105 km. We did not analyze spring migration data because of broad overlap with the austral spring equinox. These results are the first data on wintering locations, migration timing, and routes of individual migrant passerine birds that breed in South America. Given the general lack of similar data for practically all migratory birds that breed in South America, geolocator technology has the potential to revolutionize our understanding of how birds migrate—and the threats they face—on South America's rapidly changing landscape. *Received 16 April 2012, accepted 19 September 2012.*

Key words: Argentina, Fork-tailed Flycatcher, geolocator, Neotropical austral migrants, Tyrannidae, *Tyrannus savana*.

La migración a Larga Distancia de Aves en América del Sur Revelado por Geolocalizadores

Resumen.—Poco se sabe sobre la fenología de la migración, las rutas de migración, y la conectividad migratoria de la mayoría de los >230 especies de aves que se reproducen en latitudes templadas del sur de Sur América, y que luego migran hacia los trópicos para invernar. Utilizamos geolocalizadores para estudiar la migración de tres machos y tres hembras de *Tyrannus savana* capturados en sus territorios de cría en Argentina. Todas las aves iniciaron la migración de otoño entre finales de enero y finales de febrero, y migraron de 45 a 66 km dia^{-1} hacia el noroeste por el centro de América del Sur, hasta una o dos áreas de invernada. Cinco individuos primero pasaron varias semanas (en abril y mayo) en la Amazonia occidental (principalmente Perú, noroeste de Brasil, y sur de Colombia), antes de moverse hacia el este para pasar el resto de la temporada no reproductiva en el centro de Venezuela y el norte de Brasil. Un individuo estuvo principalmente en un área de invernada en el este de Colombia, noroeste de Brasil, y el suroeste de Venezuela. La migración de otoño duró aproximadamente 7–12 semanas, y cubrió una distancia de 2888–4105 km. No analizamos los datos de la migración de primavera a causa de una amplia superposición con el equinoccio de la primavera austral. Estos resultados representan los primeros datos sobre los lugares de invernada, la fenología de la migración y las rutas migratorias de individuales de aves paseriformes migratorias que se reproducen en América del Sur. Dado que existe una falta general de datos similares para prácticamente todas las aves migratorias que se reproducen en América del Sur, los geolocalizadores tienen el potencial de revolucionar nuestra comprensión de cómo las aves migran y las amenazas que enfrentan en el cambiante paisaje de América del Sur.

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EVERY YEAR, BILLIONS of birds across the planet migrate between breeding and wintering grounds (Newton 2008). These seasonal and often spectacular movements have long been studied in the Northern Hemisphere, resulting in a large body of work on migratory timing, duration, speed, and routes of many species (reviewed by Newton 2008, Faaborg et al. 2010).

By contrast, the basic natural history of bird migration in most of the Southern Hemisphere is poorly understood, largely because of the lack of infrastructure, fewer ornithologists, and the logistical challenges associated with tracking any organism across a vast scale (Jahn et al. 2009). These constraints are pronounced in South America, where >230 species migrate entirely within the continent (Stotz et al. 1996), comprising (in number of species) the third-largest bird migration system in the world (Chesser 1994, Jahn et al. 2004). Furthermore, bird migration in South America is increasingly viewed as surprisingly complex and distinct from that in North America. In particular, numerous types of bird migration exist in South America, including migration between temperate breeding grounds and the tropics, migration wholly within tropical latitudes or within temperate latitudes, elevational migration, and longitudinal migration (i.e., breeding at one longitude and wintering at another; Areta and Bodrati 2008, 2010; Cueto et al. 2011; reviewed by Chesser 1994, Joseph 1997, Faaborg et al. 2010). This wide variety of migratory strategies among species is almost certainly complicated by the tendency for sex-, age-, and population-specific variation in migratory strategies within species (e.g., Jahn et al. 2010).

It has also become increasingly apparent that theories about migration developed for species that breed at north temperate latitudes may not be directly applicable to migrants that breed in much of South America. For example, although seasonality ultimately drives migration across latitudes, the type of seasonality experienced by birds is fundamentally different between north temperate latitudes, where seasons are largely defined by variation in temperature, and most of South America, where they are largely defined by variation in rainfall. In short, migration may be motivated by different currencies in different hemispheres (Jahn et al. 2010). Even large-scale patterns of bird migration in South America are generally different from those in North America. Migrants in South America generally travel shorter distances and exhibit a greater incidence of seasonal range overlap than their North American counterparts (Chesser 1994, Stotz et al. 1996, Dingle 2008).

Given the difficulty of tracking small birds over large distances, very little information is available on migratory strategies of individual passerine birds; however, the recent and rapidly growing technological revolution in the field of animal tracking (Bowlin et al. 2010, Robinson et al. 2010, Bridge et al. 2011) presents an unprecedented opportunity to understand bird migration at an individual level and at a larger scale than was previously possible. In particular, light-level geolocators (hereafter "geolocators"), which provide daily estimates of a bird's geographic position by recording day length (Stutchbury et al. 2009, Robinson et al. 2010), have revolutionized our understanding of the movements of long-distance migrants (e.g., Heckscher et al. 2011, Bairlein et al. 2012, Seavy et al. 2012).

Data from geolocators can provide powerful tests of current theory and will likely generate new hypotheses as researchers dissect the specific circumstances associated with migratory behavior of many birds, on a daily basis, at the individual level. For example, the speed and pace of migration may be dictated by such variables as the distance of the migratory journey, season (fall or spring), and weather (Berthold 2001, Newton 2008), yet evaluating these hypotheses is practically impossible without integrated, fine-scale temporal data and large-scale spatial data. Although geolocators provide such data, the small numbers of species and individuals tracked with geolocators to date preclude meaningful tests of theory; the field is in a natural-history phase (Bodemer and Ruggeri 2012, Ricklefs 2012).

Using geolocators, we studied the migration of a long-distance migrant in South America, the Fork-tailed Flycatcher (*Tyrannus s. savana*). The nominate subspecies breeds primarily from central South America (Bolivia, Paraguay, Uruguay, and southern Brazil) to central Argentina and overwinters in northern South America (Ridgely and Tudor 1994, Chesser 1995). Their migration has been observed for decades (Zimmer 1938, Antas 1987, Capllonch et al. 2009); however, no information has been available on the migratory behavior of individuals.

Our goal was to answer the following questions. (1) What is the migration speed of Fork-tailed Flycatchers, and how does it compare with that of other passerine migrants? Given that South America presents few major topographic or hydrologic barriers to migration (Chesser 1994), migrants there should not have to fly nonstop for extended periods. We therefore expect that Fork-tailed Flycatchers generally migrate more slowly than most birds of a similar size (i.e., <100 g) on other continents. (2) What is the location and extent of the wintering range of individual Fork-tailed Flycatchers, and how does the area they occupy in winter compare to that of other passerine migrants? Recent evidence from other migrant passerines demonstrates that at least some occupy more than one area (Heckscher et al. 2011, Tøttrup et al. 2012), or move throughout winter (Beason et al. 2012).

METHODS

Study site.—We attached geolocators to 43 nesting Fork-tailed Flycatchers at Reserva Privada El Destino (35.13°S, 57.40°W), Buenos Aires Province, Argentina, during the breeding seasons (primarily November–December) of 2009 and 2010. The site is composed of temperate grasslands and marshes, intersected by woodland tracts generally dominated by Spiny Hackberry (*Celtis ehrenbergiana*) and Coronillo (*Scutia buxifolia*). The climate consists of hot summers and mild winters, with mean annual precipitation of 885 mm (n = 10 years). The rainiest months are January and February (mid- to late summer).

Field methods.—Flycatchers were captured by placing a predator model (e.g., Chimango Caracara [*Milvago chimango*]), coupled with vocalizations delivered from a portable speaker within 2 m of one or two 38-mm-mesh mist nets at a distance of 2–4 m from an active nest (except during the incubation stage, to avoid abandonment of the nest by the adult) or by placing a Fork-tailed Flycatcher model along with a conspecific call within 2 m of a mist net on a defended territory. Captured birds were banded with a numbered metal band and a unique combination of up to three Darvic color bands and were sexed as described in Pyle (1997). Eight individuals were fitted with an Mk10S geolocator (1.2 g; Fox 2010) during the 2009 breeding season, and 35 were fitted with an Mk12S geolocator (0.9 g) during the 2010 breeding season.

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Geolocators were attached using a leg-loop backpack harness (Rappole and Tipton 1991) made of Filament Kevlar (500 Tex., Saunders Thread, Gastonia, North Carolina). All birds flew well upon release. We recovered 9 geolocators in subsequent breeding seasons and were able to recover usable data from 6. None of the recaptured individuals showed any sign of injury from the geolocator or harness.

Analytical methods.—Geolocators were programmed to measure light intensity every minute but to permanently store only the maximum reading every 10 min. We estimated geolocator error by analyzing light data from the first 7 days after deployment, a period during which flycatchers were still present at the study site, typically with nestlings or fledglings. After adjusting for clock drift, we used TRANSEDIT (British Antarctic Survey [BAS], Cambridge, United Kingdom) to estimate the sun elevation that corresponded to a light threshold level of 16 (Fox 2010). This calibration resulted in a mean (± SD) error of 116.5 ± 77.1 km for the data from the 6 birds with recovered geolocators. Sunrise and sunset transitions with obvious shading events were excluded from the analysis, as well as those from 21 days before and after the austral fall and spring equinoxes (Fox 2010).

Latitude and longitude coordinates of location fixes (i.e., estimated daily location of the bird) were calculated with LOCATOR software (BAS) using midnight locations, because we assumed that the birds were most likely stationary at night (to the best of our knowledge, Fork-tailed Flycatchers migrate primarily during the day; A. E. Jahn pers. obs.). Thus, midnight locations should provide greater accuracy than midday locations, given that the bird was at the same location overnight (Fox 2010). Our construction of maps of daily locations did not include 6 coordinates that were clearly anomalous (likely because of shading): 1 far from the regular species range (in southern Chile), 3 on or off of the Pacific coast (Peru and Chile), 1 over the Atlantic Ocean, and 1 that would have necessitated movement of >1,500 km in a single day.

Light-level geolocation can estimate longitude more accurately than latitude (Fudickar et al. 2012). Therefore, similar to previous studies (e.g., Bairlein et al. 2012), we define the initiation of fall migration by a marked (i.e., ≥1°) and typically permanent change in longitude away from the study site after the breeding season. We define the last day of fall migration (and the beginning of the wintering period) as the first of at least 7 days during which the bird moved ≤3° longitude and was located ≥3° longitude from the longitude(s) that it occupied during migration. We used this conservative method to define the end of fall migration because most birds continued to move throughout winter (see below), resulting in an indistinct separation between the fall migration route and the wintering range.

We calculated distance of fall migration as the straight-line distance between the breeding site in Argentina and the first fix obtained in winter as defined above, and we calculated the speed of fall migration by dividing the fall migration distance by duration. We estimated fall migration routes using the mean of daily fixes during fall migration with Hawth's Analysis Tools for ARCGIS, version 9.3 (Beyer 2004). We used a minimum of 6 fixes bird^{-1} during the entire migration period. We were unable to estimate the location of the fall migration route of two birds (C and F) because we obtained ≤2 fixes during fall migration for each, or for another (E) because there were no fixes >600 km from the study site. We were unable to document the timing and route of spring migration because of broad overlap with the austral spring equinox.

We created a spatially explicit description of the winter distribution of each bird using kernel density estimator analysis (Silverman 1986, Terrell and Scott 1992) in the Spatial Analysis tool of ARCMAP, version 9.3 (ESRI, Redlands, California). We set the search radius at 200 km and grid cell size at 2 km (Bächler et al. 2010, Ryder et al. 2011) and required ≥24 coordinates to estimate the winter distribution of each bird. For each individual, we present kernel densities encompassing >50%, 50–70%, and 70–95% of the maximum density. We used 21 days prior to the austral spring equinox as the cutoff date for the analysis of winter range, because of the difficulty associated with estimating the location of the bird near the equinox. Results are presented as means ± SD.

Results

Fork-tailed Flycatchers at our study site in Argentina breed primarily from late November to mid-January. Individuals with geolocators initiated fall migration between late January and late February and migrated 2,888–4,105 km during a period of 48–84 days (Table 1), arriving on the winter grounds in mid-April (Fig. 1). The typical route of migration was northwest through Uruguay and northeastern Argentina, then across central South America (Paraguay and Bolivia) to northern South America (Fig. 1). All 3 birds appeared at times to reverse direction during fall migration (Fig. 1), although we are uncertain whether these movements are actual or due to calculation error (e.g., associated with proximity to the austral fall equinox).

The maximum speed was 66 km day^{-1}, and the average speed among the 6 birds was 55 ± 9.8 km day^{-1} (Table 1). Average migration speed of males (57 ± 8.4 km day^{-1}) was slightly higher than that of females (52 ± 12.2 km day^{-1}). Although these speeds are not significantly different from each other (Wilcoxon test for independent samples, $W = 12.5$, $P = 0.60$), the small sample size precludes definitive conclusions. On average, females migrated 3,588 ± 628.7 km and males migrated 3,440 ± 452.3 km.

After fall migration, 5 of 6 individuals occupied two wintering areas in succession. The first was in western Amazonia (i.e., primarily Peru, northwestern Brazil, and southern Colombia), where they remained 8–39 days during mid-April to late May (Fig. 1). They

Table 1. Initiation, duration, distance, and speed of fall migration of 3 male and 3 female Fork-tailed Flycatchers captured at Reserva Privada El Destino, Argentina. Initiation of fall migration is the first date on which there was a change of ≥1° longitude in relation to that of the breeding site. Distance is the straight-line distance between the breeding site and the first fix obtained in winter. Speed represents the distance of migration divided by duration of migration in days.

ID	Sex	Initiation	Duration (days)	Distance (km)	Speed (km day^{-1})
A	M	8 February 2011	65	3,195	49
B	M	5 February 2011	69	3,962	57
C	M	27 February 2010	48	3,163	66
D	F	11 February 2011	62	4,105	66
E	F	24 January 2010	84	3,770	45
F	F	13 February 2011	64	2,888	45

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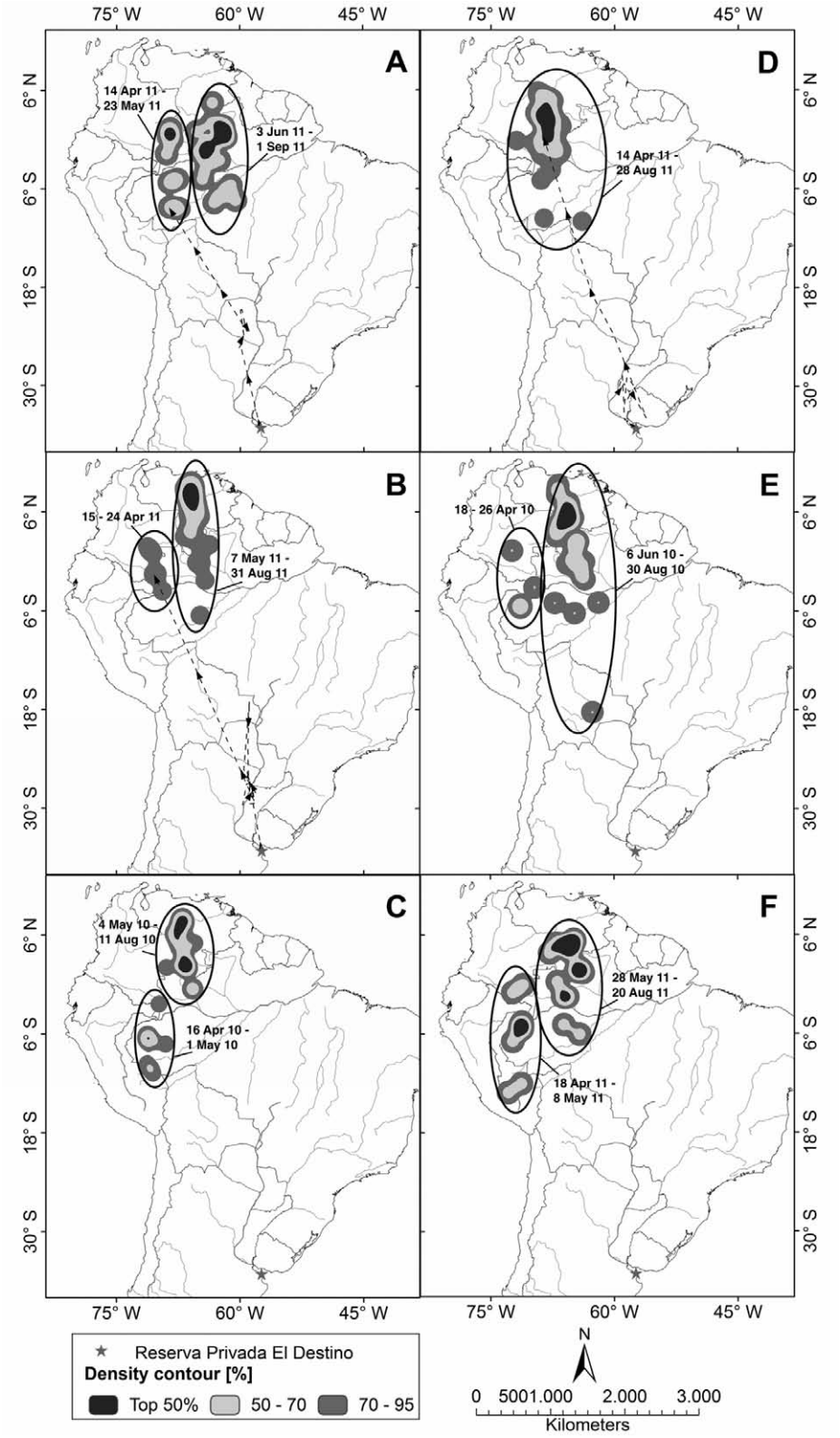


FIG. 1. Winter range and associated error (>50%, 50–70%, and 70–95% kernel densities) and fall migration routes of 6 Fork-tailed Flycatchers initially captured at Reserva Privada El Destino, Argentina (star). The individual identifier of each is at the top right of each map. Locations and dates of first and second wintering areas are indicated. Dates between these two periods are those for which we have no data. Fall migration routes from 3 birds are missing because of lack of data during that period. Lines depicting the migration routes do not always represent the exact migration route because of gaps in dates of location fixes due to the austral fall equinox and shading events (see text).

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then moved >800 km east to central Venezuela and northern Brazil, where they stayed 84–136 days before sampling was ended because of the proximity of the austral spring equinox (Fig. 1).

Discussion

The 6 Fork-tailed Flycatchers in our study all left the breeding site in Argentina within a 1-month period and migrated <70 km day^{-1}. The 3 individuals for which we had migratory-route data migrated northwest in fall, primarily through northern Argentina, Paraguay, and Bolivia, which corroborates previous records of this species as passage migrants in Bolivia from February to April (Davis 1993, Chesser 1997).

Fall migration speeds of Fork-tailed Flycatchers in our study were generally lower than those of Purple Martins (*Progne subis*; >150 km day^{-1}; Stutchbury et al. 2009), European Hoopoes (*Upupa epops epops*; >81 km day^{-1}; Bächler et al. 2010), Veeries (*Catharus fuscescens*; 82 km day^{-1}; Heckscher et al. 2011), Northern Black Swifts (*Cypseloides niger borealis*; 341 km day^{-1}; Beason et al. 2012), Red-backed Shrikes (*Lanius corullio*; 101 km day^{-1}; Tøttrup et al. 2012), Northern Wheatears (*Oenanthe oenanthe*; 88–160 km day^{-1}; Bairlein et al. 2012, Schmaljohann et al. 2012), and congeneric Eastern Kingbirds (*T. tyrannus*), Western Kingbirds (*T. verticalis*), and Scissor-tailed Flycatchers (*T. forficatus*; all >90 km day^{-1}; Jahn et al. 2013). However, they are similar to fall migration speeds of Wood Thrushes (*Hylocichla mustelina*; 27–106 km day^{-1}), though these values were calculated by including stopover days, which can be prolonged before and after a Wood Thrush crosses the Gulf of Mexico in fall (Stutchbury et al. 2009).

Our results, therefore, generally support our expectation that Fork-tailed Flycatchers migrate more slowly than migrants of a similar size, which may be attributed, in part, to the lack of major topographical barriers in South America, such as deserts or large bodies of water. Additionally, Fork-tailed Flycatchers migrate primarily during the day and, presumably, must devote a portion of daylight hours to foraging. By contrast, nocturnal migrants such as Red-backed Shrikes can migrate at night and refuel during the day (Tøttrup et al. 2012). This argument for why diurnal migrants travel more slowly than nocturnal migrants does not hold, however, for Purple Martins and Northern Black Swifts, diurnal migrants that travel vast distances per day on migration. We suggest that they are able to travel more quickly because their morphology allows for high velocities and their foraging behavior allows for simultaneous feeding and flying. Fork-tailed Flycatcher morphology, on the other hand, may be better suited for slower velocities and maneuverability associated with foraging by sallying from a perch.

All but one of the birds we studied used two wintering areas, a pattern similar to that of several other migrants that appear to occupy sequential areas during the non-breeding season. Two congeners of Fork-tailed Flycatcher, Eastern and Western kingbirds, also use more than one wintering area, with Eastern Kingbirds occupying northwestern South America at the same time (April) that Fork-tailed Flycatchers occupy this general region (Jahn et al. 2013). Veeries use two wintering areas in Amazonia, perhaps following local increases in food abundance associated with river flooding across the Amazon Basin (Heckscher et al. 2011). Similarly, Northern Black Swifts overwinter in Amazonia and have large winter distributions, with a tendency to move westward toward the end of the non-breeding season (Beason et al. 2012). Red-backed Shrikes likewise first use the Sahel savanna of Sudan for ≤2 months after breeding, before moving farther south for the rest of the winter (Tøttrup et al. 2012). Taken together, the results of these studies and our own suggest that large-scale (i.e., hundreds to thousands of kilometers) movements of overwintering migrants in the tropics may be more common than was previously thought.

We propose that the use of two wintering areas in South America is related to spatial and temporal variation in rainfall across the Amazon Basin. Rainfall appears to be important in maintaining adequate food supplies for migrating and overwintering insectivorous migratory birds in both the Neotropics and Paleotropics (Sinclair 1978, Hutto 1985, Sherry and Holmes 1996, Herremans 1998, Brown and Sherry 2006, Tøttrup et al. 2012). Rainfall is at or near its annual peak in April in northwestern Amazonia (i.e., the first winter area of the birds we tracked) when the birds arrive there (Fig. 1). Rainfall in that region begins to decrease in June, by the time the birds have moved east to extreme northern Brazil and central Venezuela, where rainfall peaks in June and July (Poveda et al. 2006, Espinoza et al. 2009) and where the birds spend the rest of winter.

Another explanation for the use of two wintering areas could be related to postbreeding molt. In North America, congeneric Western Kingbirds exhibit a molt-migration in fall. Adults migrate to the region of the Mexican monsoon (Arizona–northern Mexico), where they molt primary flight feathers before proceeding farther south to overwinter (Barry et al. 2009, Jahn et al. 2013). Presumably, they do so to take advantage of a temporal window of food abundance associated with the Mexican monsoon (Rohwer et al. 2005). Fork-tailed Flycatchers also molt primarily during the non-breeding season (Zimmer 1938, A. E. Jahn pers. obs.), although the exact timing of the molt and how it varies across the winter range remain unknown.

Our study represents the first tracking of individual passerine migrants that breed in South America, and demonstrates that individual Fork-tailed Flycatchers can occupy all three major watersheds on the continent—Río de la Plata, Amazon, and Orinoco River basins—and up to eight countries on an annual basis (Fig. 1). We also demonstrate the feasibility of using geolocators to better understand the annual cycle of migratory birds within South America. Among short- to medium-distance migrants, geolocators are likely most useful for species that migrate wholly at temperate latitudes (i.e., Patagonia) because geolocator data are most accurate at higher latitudes. Additionally, given that location estimation based on longitude provides a relatively good estimate of movement, even for short-distance migrants (Fudickar et al. 2012), geolocators can provide novel information about the annual cycle of short-distance longitudinal migrants in South America (Areta and Bodrati 2008, 2010).

Geolocators can be used in South America to address many basic and important questions, including the following. (1) What are the potential carryover effects between the non-breeding season in northern South America and the breeding season at south temperate latitudes? (2) What potential benefits do migratory birds gain from occupying two areas after fall migration? For example, do they undergo a molt at the first site (as in

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molt-migration; Rohwer et al. 2005) and/or benefit from higher food abundance there? And (3) what are the migration routes, timing of migration, speed of migration, and winter distributions of other migratory bird populations in South America? Until such basic data are collected, the mechanisms that underlie the evolution and regulation of bird migration in South America cannot be adequately addressed (Cavalcanti 1990, Jahn et al. 2006, Alves 2007). More generally, comparisons across migratory systems, hemispheres, and continents promise a better understanding of the mechanisms that drive avian migratory strategies across the planet (Dingle 2008, Jahn and Cueto 2012).

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