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ARTICLE

Intra-tropical migration and wintering areas of Fork-tailed Flycatchers (*Tyrannus savana*) breeding in São Paulo, Brazil

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ABSTRACT: Fork-tailed Flycatchers (*Tyrannus s. savana*) breed from central to southern South America from September to January, migrating to northern South America to spend the non-breeding season. However, little is known of the migratory routes, rate, and timing of migration of those that breed in Brazil. In 2013, we attached light-level geolocators to breeding Fork-tailed Flycatchers breeding in São Paulo State. Data for six male flycatchers recaptured in 2014 indicates that they exhibited two fall migration strategies. Some individuals migrated northwest to the wintering grounds (primarily Colombia, Venezuela and northern Brazil), while others first spent several weeks in southwestern Brazil before going to the wintering grounds. Mean fall migration rate was 69 km/day (±13.7) during 59 (±13.2) days. Some flycatchers moved during winter, using more than one winter area. Flycatchers initiated spring migration in July and migrated southeast to the breeding grounds at a mean rate of 129 km/day (±19.0) during 27 (±2.8) days. A detailed understanding of the annual cycle of South America's migratory birds is essential to evaluating theoretical questions, such as the evolution of their life history strategies, in addition to applied questions, such as explanations for changes in population size, or their role as disease vectors.

KEY-WORDS: austral, Cerrado, Itirapina, molt, Neotropical.

INTRODUCTION

The Fork-tailed Flycatcher (*Tyrannus savana*) is a widespread Neotropical species, occurring from Mexico to Argentina and much of lowland South America east of the Andes Mountains, from the northern coast of the continent south to central Argentina (Fitzpatrick *et al.* 2004, Jahn & Tuero 2013). The nominate subspecies (*T. s. savana*) breeds from central Brazil to south-temperate latitudes in Argentina, and overwinters in northern South America (primarily in the Orinoco River Basin and the northern Amazon River Basin; Chesser 1995, Fitzpatrick *et al.* 2004, Jahn & Tuero 2013, Jahn *et al.* 2013a).

Although the Fork-tailed Flycatcher is a widespread and relatively common species in South America, decades of observations have provided few details on its migratory routes or wintering areas (Zimmer 1938, Antas 1987, Capllonch *et al.* 2009). This is also true of many other Neotropical austral migrants, which breed and migrate (typically wintering to the north of where they breed) within South America (Chesser 1995, Jahn *et al.* 2004, Cueto & Jahn 2008). Although Brazil has long been recognized as an important crossroads for migratory birds (Sick 1983, Alves 2007), bird migration in Brazil has been understudied (Antas 1987, Cavalcanti 1990, Alves 2007). Indeed, almost all research on Neotropical austral bird migration in Brazil is in a descriptive stage, focused on answering such questions as how many migratory species there are and where they migrate (Alves 2007).

Understanding bird migration in Brazil is important not only for local and national research, education and conservation planning, it is also important at a continental scale. Brazil accounts for almost half (43%) of South America's landmass, and 73% of Neotropical austral migrant bird species (233 total) occur in the country (Parker *et al.* 1996). Therefore, improving our understanding of how birds migrate within and between Brazil and other countries holds significant potential for improving our knowledge of and ability to develop conservation plans for migratory birds across South America.

Previous research on the movements of Fork-tailed

Flycatchers indicate that those breeding in Buenos Aires, Argentina migrate from late January to April after breeding (November–January) through the center of the continent (northern Argentina, Bolivia, Paraguay) to northwestern South America to overwinter (Jahn *et al.* 2013a). Fork-tailed Flycatcher has been recorded as a passage migrant in Bolivia from February to April (Davis 1993, Chesser 1997), and again on its return south, from September to November (Chesser 1997). Within Brazil, the nominate subspecies breeds in the Planalto Central (central highlands) from September to December (Pimentel 1985, Marini *et al.* 2009), thereafter migrating to the wintering grounds in January and February (Alves 2007). The lack of records of the species around Brasilia after early February suggests that the fall migration route of southern breeding populations of Fork-tailed Flycatcher does not pass through central Brazil (Antas 1987, Alves 2007).

Our objective was to describe the migratory timing (begin and end dates, rate and duration), routes and wintering areas of individual Fork-tailed Flycatchers (hereafter, "flycatchers") breeding in southeastern Brazil. This represents a first step towards understanding the full annual cycle of this common migratory species.

METHODS

We captured flycatchers at the Estação Ecológica de Itirapina, São Paulo State (22.3°S; 47.9°W) from 11 to 27 of November 2013. This site is primarily composed of campo and cerrado grassland and gallery forest along streams. Flycatchers breed there from October to January (A.E. Jahn, unpub. data) and are absent from March to July (Willis 2004).

Flycatchers were captured by placing a predator model (*e.g.*, Savanna Hawk, *Buteogallus meridionalis*), or a speaker emitting a flycatcher call next to one or two 3 × 12 or 3 × 18 m polyester or nylon mist nets (38 mm mesh size). Nets were placed within an active flycatcher territory, usually 1–3 m from an active nest. Captured flycatchers were held in cotton bags before being banded using techniques described in Ralph *et al.* (1993). Flycatchers were aged using the presence of juvenile plumage, and sexed using the shape of the notch of primaries 8–10, or the presence of a brood patch or cloacal protuberance (Pyle 1997). Before release, flycatchers were fitted with a model IntiGeo P64 light-level geolocator (MigrateTech, Inc., Cambridge, UK) using a backpack-style harness (Rappole & Tipton 1991) made of Filament Kevlar (500 tex; Saunders Thread, Gastonia, North Carolina, USA).

Data analysis

We used R-package GeoLight (Lisovski & Hahn 2012) to process light data, identifying sunrise and sunset times using a light threshold of 15, and eliminating outliers using the loessFilter function to delete twilight transitions exceeding the interquartile range of residuals from a smoothed line. We calibrated light data using the first 20 days after the bird was released and excluded latitude estimates for 20 days before and after the vernal and autumnal equinoxes. Finally, we used a distance filter to exclude locations that required movements between consecutive positions in excess of a continuous rate of 20 km/h.

We identified departure and arrival dates by combining information about periods of movement and residency generated from twilight times and from latitude and longitude data. Periods of movement and residency were calculated using the changeLight function, with a probability of change of 0.8 and a minimum stationary period of 3 days. Because this method is based on changes in sunset and sunrise times, it can be used to infer the beginning and end of migration even around the equinox when latitudinal estimates are unreliable. We identified wintering locations by averaging latitude and longitude between 15 May and 1 July due to little evidence of movement during these dates and because these dates were far enough from the equinox that we could calculate latitude and longitude.

Because we defined distance of migration as the straight-line distance between the breeding site and the wintering area, reported migration distances are minimum distances. Likewise, the migration rates we report represent minimum rates because we defined migration rate in spring or fall as the distance of migration divided by the duration of migration (including stopovers) during each period. Summary statistics represent means ± standard error (SE).

RESULTS

In 2013, we deployed geolocators on 29 adult flycatchers (12 females and 17 males). In the 2014 breeding season, we recovered six geolocators, all from males. However, in that season we also observed, but were not able to recapture, an additional 3 males and 5 females that had been outfitted with geolocators in 2013. Females were more difficult to capture and recapture than males because they did not attack the predator model or respond to playback as aggressively as did males. Thus, the return rate of flycatchers with geolocators (*i.e.*, which were recaptured or re-observed in 2014) was 48.3% (14 of 29 flycatchers), which is similar to that of some other songbird species deployed with geolocators (*e.g.*, 44.7% return rate for Scissor-tailed Flycatchers, *Tyranus forficatus*; Jahn *et al.* 2013b).

The six birds initiated fall migration between mid-January and mid-February of 2014 (Table 1), with most migrating northwest across central or western Amazonia (western Brazil and eastern Bolivia) to wintering grounds in northern South America (Figure 1). However, two flycatchers (H527 and H595) first moved southwest to the region of the border of Brazil (Mato Grosso do Sul, Paraná states), Paraguay and northeastern Argentina, thereafter migrating to the wintering grounds (Figure 1). Fall migration ended between early March and mid-May (Table 1) and lasted 59 (13.2) days, during which flycatchers migrated at a rate of 69 (13.7) km/day (Table 2).

Some flycatchers initially overwintered in the region of northern Peru, northwestern Brazil (Amazonas) and southern Colombia (*e.g.*, H565, H595, H607; Figure 1) or in the region of eastern Colombia, western Venezuela and northern Brazil in Amazonas (*e.g.*, H524, H527, H548; Figure 1). The mean distance between the breeding site and the wintering area for the six flycatchers was 3169 (45.4) km (Table 2).

One flycatcher (H548) remained sedentary throughout winter whereas others (H524, H565, H595, H607) used multiple overwintering areas, moving in a northeasterly direction between March and July (Figure 1). One bird (H527) moved eastwards before returning south in spring (Figure 1).

Spring migration began in late July and August (Table 1) and lasted 27 (2.8) days, during which flycatchers generally migrated over central Amazonia in a southeasterly direction at a rate of 129 (19.0) km/day (Table 2). Some birds appeared to use spring stopover sites before arriving at the breeding grounds (*e.g.*, H565, H595; Figure 1). Three birds (H548, H595, H607) were located to the southwest of the breeding site before arriving there (Figure 1), though this could be due to light measurement error. In particular, point locations over the Atlantic Ocean (H527, H607, Figure 1) are likely due to geolocator light measurement errors. Birds arrived at the breeding site between 30 August and 9 September (Table 1).

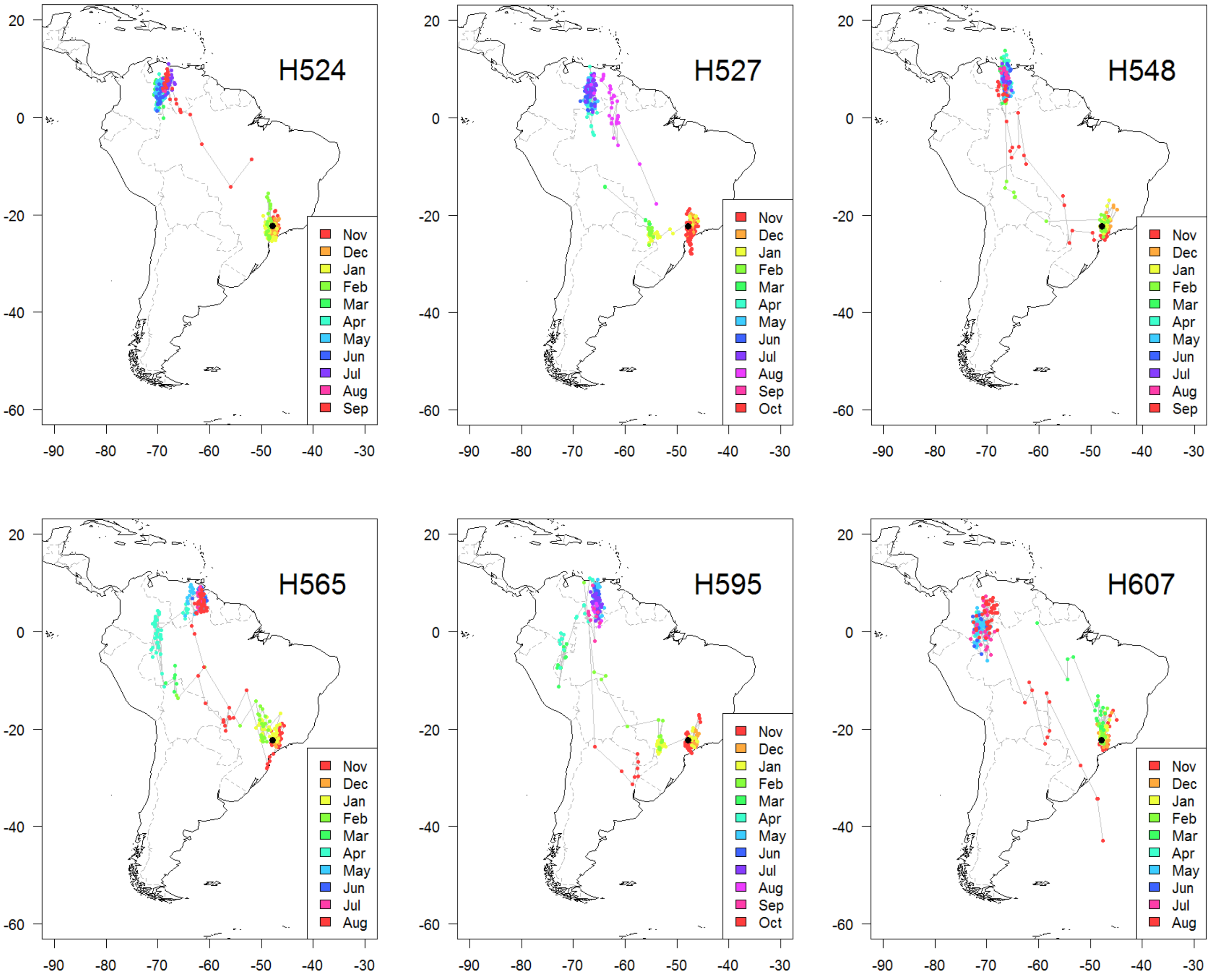

FIGURE 1. Wintering areas and migration routes of six male Fork-tailed Flycatchers captured at a breeding site in São Paulo, Brazil. Alphanumerical combinations in each map correspond to the individual ID for each bird in Tables 1 and 2. Point locations that occur over the Atlantic Ocean are likely due to geolocator light measurement errors.

TABLE 1. Fall and spring migration initiation and termination dates for six male Fork-tailed Flycatchers captured at a breeding site in São Paulo, Brazil, in 2013 and tracked in 2014. "ID" is the alphanumerical combination used to identify individuals in Figure 1.

ID	Fall migration		Spring migration	
	Begin date	End date	Begin date	End date
H524	19 Feb	8 Apr	21 Aug	5 Sep
H527	15 Jan	3 Mar	14 Aug	9 Sep
H548	12 Feb	16 Mar	7 Aug	2 Sep
H565	8 Feb	13 May	2 Aug	30 Aug
H595	16 Jan	30 Apr	11 Aug	8 Sep
H607	13 Feb	13 Mar	25 Jul	30 Aug
Mean	3 Feb	3 Apr	8 Aug	3 Sep

TABLE 2. Individual migration history (distance, duration and rate of migration in fall and spring) of six male Fork-tailed Flycatchers captured at a breeding site in São Paulo, Brazil. "ID" is the alphanumerical combination used to identify individuals in Figure 1. Migration distance represents the straight-line distance between the breeding site and the wintering area. Migration rate is calculated as the distance of migration divided by the duration of migration during each period. Summary statistics represent means ± standard error (SE).

ID	Distance (km)	Fall migration		Spring migration	
		Duration (days)	Rate (km/day)	Duration (days)	Rate (km/day)
H524	3293	48	69	15	220
H527	3166	47	67	26	122
H548	3255	32	102	26	125
H565	2990	94	32	28	107
H595	3214	104	31	28	115
H607	3098	28	111	36	86
Mean (SE)	3169 (45.4)	59 (13.2)	69 (13.7)	27 (2.8)	129 (19.0)

DISCUSSION

Overall, results indicate that male Fork-tailed Flycatchers breeding in southeastern Brazil initiate fall migration in January or February, with some migrating directly to wintering grounds, whereas others first spend time in the region of southern Brazil, Paraguay and northeastern Argentina before migrating to northern South America. All birds overwintered from March to July in either northern Amazonia or the Orinoco Basin (Colombia and Venezuela), with some remaining sedentary and others moving northeasterly or easterly during winter. Beginning in late July, flycatchers returned southeastwards in spring across the Amazon Basin to São Paulo.

That flycatchers migrated in fall through western Brazil and eastern Bolivia corroborates a historical lack of records of the species in Brasilia after the second week of February (Antas 1987). Flycatchers overwintered primarily in western and northern Amazonia and the Orinoco Basin, similar to results of previous research on the migration of Fork-tailed Flycatchers breeding in Buenos Aires, Argentina (Jahn *et al.* 2013a), suggesting that this is an important wintering area for various Fork-tailed Flycatcher populations. A large part of this winter range is composed of grasslands ("llanos") that are structurally similar to the cerrado grasslands that flycatchers occupy during the breeding season in central Brazil.

A notable and unexpected finding is that some flycatchers spend several weeks southwest of the breeding site prior to migrating to the wintering grounds. We do not yet know the reason for this, but it is similar to the movements of some species breeding in western North America, such as Western Kingbirds (*Tyrannus verticalis*; Barry *et al.* 2009, Jahn *et al.* 2013b) and Western Tanagers (*Piranga ludoviciana*; Butler *et al.* 2002), which go to northwestern Mexico to molt in late summer (Rohwer *et al.* 2005). Indeed, the use of miniaturized tracking devices and stable isotopes in feathers molted during winter has provided evidence showing that distinct movements that are separated by layovers is more common among passerine migrants during fall migration and winter than previously thought (McKinnon *et al.* 2013).

That spring migration was faster than fall migration is similar to that of congeneric Western Kingbirds and

Scissor-tailed Flycatchers that breed in North America (Jahn *et al.* 2013b), and has been found in other migratory taxa (McKinnon *et al.* 2013). Flycatchers are potentially under a time-selected schedule during spring migration due to positive selection to arrive, establish territories and find mates as early as possible on the breeding grounds, resulting in faster migration compared to fall. Because Fork-tailed Flycatchers undergo an annual molt primarily during winter (Pyle 1997), fall migration of flycatchers that breed in Brazil may be timed so that their arrival on the wintering grounds coincides with resource peaks at different parts of the continent, therefore acquiring the necessary food resources to molt, as has been suggested for populations that breed in Argentina (Jahn *et al.* 2013a).

Intriguing questions for future research include: 1) What obstacles to migration exist in South America and how are austral migrants adapted to face them? For example, since flycatchers in this study are primarily grassland species, does the Amazon Rainforest, which covers a large part of their migratory route, act as a barrier to their migration?; 2) How did different migratory strategies evolve among populations with different life history strategies (*e.g.*, clutch size)? Flycatchers breeding at tropical latitudes of South America lay on average one less egg than those at South-temperate latitudes in Argentina (Jahn *et al.* 2014). If tradeoffs exist between investment in migration *vs.* reproduction, such variation in investment in reproduction could potentially lead to different migration strategies among populations; and 3) What is the behavioral and physiological ecology of birds that migrate within South America, in comparison to those that breed on other continents? For example, some migratory songbirds in North America switch from consuming arthropods during the breeding season to consuming fruit during fall migration (Parrish 1997). Is this how post-breeding migration is fuelled in ecologically- and taxonomically-similar South American migrants?

South America, the epicenter of avian diversity on the planet, offers an exceptional opportunity to study bird migration. Given that at least 230 bird species migrate entirely within the continent, bird migration within South America represents – in terms of number of species – the largest bird migration system in the Southern Hemisphere (Chesser 1994, Stotz *et al.* 1996, Jahn *et al.* 2004). Furthermore, patterns of bird migration in South America are highly diverse and include (1) temperate-tropical migration (*i.e.*, breeding at temperate latitudes and wintering at tropical latitudes), (2) intra-tropical migration, and (3) longitudinal migration, in which birds breed at one longitude and overwinter at another (Areta & Bodrati 2010). As a result, future descriptive and theoretical research on these diverse types of migration offers novel insights into why and how birds migrate (Jahn & Cueto 2012). Research on the full annual cycle of migratory bird species within and between countries in South America should be prioritized, since such information is essential to develop effective management and conservation plans for these species in an era of rapid global change.

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