Variable Seasonal Movement Dynamics among Individual Snail Kites (Rostrhamus sociabilis) in South America

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VARIABLE SEASONAL MOVEMENT DYNAMICS AMONG INDIVIDUAL SNAIL KITES (*ROSTRHAMUS SOCIABILIS*) IN SOUTH AMERICA

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Abstract.—South America is home to the highest diversity of birds on the planet, yet we still understand relatively little about their seasonal movements, or even which species are migratory. During two consecutive years, we used satellite transmitters to study the movement ecology of 10 individual Snail Kites (*Rostrhamus sociabilis*) captured in southern Brazil. We detected highly variable movement patterns among Snail Kites, with some migrating between two well-defined sites, migrating up to 4000 km to the mouth of the Amazon River. Others exhibited nomadic/facultative movements, moving different distances and to different sites

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between seasons and years. Overall, Snail Kites spent most of the migration period at stopover sites, moved at a higher speed, and used fewer stopovers in austral spring than in fall. These results provide the first evidence that Snail Kites in South America move across large distances, effectively connecting major watersheds, and suggest that individual Snail Kites are highly flexible in how they track resources over time and space. The complex movements and highly variable migratory behavior we detected among Snail Kites points to the need for more detailed research on the behavioral ecology and risks to survival across the annual cycle and broad range of this enigmatic and poorly understood species.

KEY WORDS: *Snail Kite*; Rostrhamus sociabilis; *austral migration*; *Brazil*; *nomadic*; *raptor*; *satellite transmitter*; *waterbird*.

DINÁMICA DE MOVIMIENTOS ESTACIONALES VARIABLES ENTRE INDIVIDUOS DE *ROSTRHAMUS SOCIABILIS* EN SUDAMÉRICA

RESUMEN.—Si bien Sudamérica alberga la mayor diversidad de aves del planeta, todavía entendemos relativamente poco sobre sus movimientos estacionales e incluso qué especies son migratorias. Durante dos años utilizamos transmisores satelitales para estudiar la ecología del movimiento de diez individuos de *Rostrhamus sociabilis* capturados en el sur de Brasil. Detectamos patrones de movimiento muy variables entre individuos, con algunos ejemplares migrantes entre dos lugares bien definidos, migrando 4000 km hasta la desembocadura del río Amazonas. Otros exhibieron movimientos nómadas/facultativos, moviéndose diferentes distancias y a diferentes sitios entre estaciones y años. En general, los individuos que estudiamos pasaron la mayor parte del período de migración en lugares de asentamiento temporal y se desplazaron a mayor velocidad y utilizaron menos paradas en la primavera austral que en el otoño. Estos resultados proporcionan la primera evidencia de que esta especie se mueve en América del Sur a través de grandes distancias, conectando eficazmente las principales cuencas hidrográficas, y sugieren que los individuos de *R. sociabilis* en América del Sur son muy flexibles en la forma en que siguen la disponibilidad de recursos a través del tiempo y el espacio. Los movimientos complejos y el comportamiento migratorio altamente variable que detectamos entre individuos de *R. sociabilis* destacan la necesidad de realizar investigaciones más detalladas sobre su ecología y comportamiento, como también entender los factores de riesgo para su supervivencia a lo largo del ciclo anual dentro del amplio rango de distribución de esta enigmática y poco estudiada especie.

[Traducción de los autores editada]

INTRODUCTION

Birds move within and between all major ecosystems on the planet. However, the timing, routes, and proximate and ultimate mechanisms underlying the movements of most species are still poorly understood (Newton 2008). In particular, movements across the annual cycle of birds that breed in the southern hemisphere have been little studied. Within South America alone, numerous bird species breed at temperate latitudes, then overwinter closer to the Equator (i.e., Neotropical austral migration; Chesser 1994, Jahn et al. 2020). Although the majority of Neotropical austral migrants are passerines, such as Fork-tailed Flycatchers (*Tyrannus savana*; Jahn et al. 2019) and White-crested Elaenias (*Elaenia albiceps chilensis*; Bravo et al. 2017), nonpasserine birds such as waterbirds and raptors make up a substantial portion of Neotropical austral migrants (e.g., Antas 1994, Chesser 1994, Capllonch 2004, 2018). For example, the Ruddy-headed Goose (*Chloephaga rubidiceps*) migrates between Patagonia and the Pampas grasslands of southern South America (Pedrana et al. 2020). Others are intratropical migrants, such as the Orinoco Goose (*Neochen jubata*), which migrates wholly within tropical latitudes of the continent (Davenport et al. 2012). Other species migrate between inland breeding sites in South America and sites along the Pacific or Atlantic coasts (e.g., Black Skimmers [*Rynchops niger*]; Davenport et al. 2016).

To date, at least 23 species of raptors have been identified as migratory within South America (Chesser 1994, Hayes et al. 1994, Zalles and Bildstein 2000). Patterns of Neotropical austral raptor migration, however, are generally not as conspicuous as Nearctic-Neotropical raptor migration. For example, Mississippi Kites (*Ictinia mississippiensis*), Broad-winged Hawks (*Buteo platypterus*), Swainson's Hawks (*Buteo swainsoni*), and Turkey Vultures (*Cathartes aura*) occur by the hundreds to thousands at some locations during migration (Bildstein 2004). In contrast, Neotropical austral migrant raptors are generally inconspicuous during migration, in part due to smaller population numbers and because of the lack of migration bottlenecks within South America (Bildstein 2004). Additionally, a lack of standardized raptor migration monitoring in South America may contribute to underestimates of their movements (Juhant 2012). Yet, a growing body of evidence shows that more species of raptors are Neotropical austral migrants than was previously thought. Juhant (2011) estimates that 45 species (almost half) of raptors in South America migrate within at least part of their range. Lees and Martin (2015) found that the Rufous-thighed Kite (*Harpagus diodon*) is migratory within Brazil, and Olivo (2003) reported that the White-tailed Hawk (*Geranoaetus albicaudatus*) migrates through the center of the continent. Additionally, Zilio et al. (2014) reported that the White-tailed Hawk, previously thought to be resident in southeastern South America, is actually partially migratory.

A notable exception to the rather cryptic nature of Neotropical austral raptor migration is the Snail Kite (*Rostrhamus sociabilis*), which occurs by the thousands during migration at some localities in South America (Capllonch 2004). Snail Kites occur from Florida, USA, to Argentina (BirdLife International 2020), with the nominate subspecies being widespread and found from Central America to central Argentina (Reichert et al. 2020). Snail Kites are highly social semicolonial breeders, nesting and foraging in freshwater wetlands, including shallow lake edges and freshwater marshes (Reichert et al. 2020) that are usually characterized as palustrine-emergent wetlands with long hydroperiods (Cowardin et al. 1979). Vegetation typically is interdigitated throughout such wetlands, with low trees and shrubs often interspersed (Cowardin et al. 1979, Bergmann et al. 2013). Snail Kites search for prey, primarily *Pomacea* spp. snails (Magalhães 1990), from a perch or in flight. Upon capturing a snail, a kite typically takes it to a perch, extracts the body and albumen gland from the hard shell, and consumes it (Vaz-Ferreira et al. 1965).

As is true of most migratory birds in South America, we know little about the population- and individual-level movement patterns of Snail Kites there, including their temporal and spatial migratory connectivity (i.e., the proportion of a breeding population that overwinters together, and the migratory routes they use; Webster et al. 2002, Bauer et al. 2016, Cohen et al. 2018). Although Snail Kites are thought to move substantial distances within South America, with large numbers moving along the Paraguay River and Atlantic coast, the origins and destinations of individual Snail Kites remain uncertain (Hayes 1991, Sick 1997, Bildstein 2004). Antas (1994) and Capllonch (2018) have suggested that Snail Kites migrate between Argentina (and/or southern Brazil) and the Pantanal, a large wetland ecosystem on the border between Brazil and Bolivia. In northern Argentina, Snail Kites are seen migrating in large numbers in May and June (Capllonch 2004), and are observed arriving in Uruguay in September then departing in April (Arballo and Cravino 1999). It is thought to be a partial migrant in southern Brazil (Albuquerque et al. 1986, Belton 1994, Bencke 2001, Zilio et al. 2014) and the Chaco ecoregion of Argentina and Paraguay (Short 1975, Hayes 1991). Nevertheless, its movements are unpredictable, as the species may be abundant in a given region in one year, but scarce in other years (L. Bugoni unpubl. data) and potentially driven by droughts (Di Giacomo and Krapovickas 2005).

Information on individual Snail Kite movements in South America could provide important insights about the times of year they are most vulnerable, given the substantial changes facing this species across its range. Major river systems such as the Amazon and the Paraná-Paraguay are undergoing unprecedented transformations as a result of various anthropogenic activities, which is true of other large river systems across the planet (Best 2019). Within the Amazon Basin alone, dozens of dams are currently being built or are planned across the Amazon Basin, with subsequent hydrophysical and biotic impacts that are yet to be fully understood (Latrubesse et al. 2017). Although the Snail Kite is currently listed as “Least Concern” in terms of extinction risk, with increasing population numbers (BirdLife International 2020), climate-related habitat changes are expected across its range (e.g., Tassi et al. 2013). Thus, knowledge about its movement ecology will provide vital information about when, where, and what key habitat resources Snail Kites use during their annual cycle. For example, evidence of strong migratory connectivity could provide vital information about the wetlands that large numbers of Snail Kites use in different seasons and thus help prioritize monitoring and protection of both Snail Kites and the wetlands that are important to their populations. Additionally, because Snail Kites are known to forage in rice fields (Dias and Burger 2005) where potentially harmful pesticides are used (Parsons et al. 2010), a more detailed understanding of their annual cycle could inform future conservation action in agricultural landscapes.

We here provide the first description of movement patterns of Snail Kites in South America throughout their annual cycle. Specifically, we aimed to understand their full annual cycle, including the timing and rate of seasonal movements, routes used while moving between sites, and variation in movements between years. Based on these results, we discuss future directions for both basic and applied research on this poorly studied species in the Neotropics.

METHODS

Study Area. We captured Snail Kites from 20–22 November 2017 at Taim Ecological Station, a federally protected reserve of approximately 33,000 ha in the state of Rio Grande do Sul, Brazil (32.70°S, 52.62°W), a region of the country where Snail Kites are common breeders (Belton 1984). We chose this site because breeding Snail Kites had been observed at this site across multiple years and because it represents the largest known breeding colony in the region (L. Bugoni unpubl. data), which increased our chances of capturing a sufficient number of Snail Kites in a relatively short period of time. This site is dominated by interconnected wetland habitats with lagoons, vegetated marshes, and canals; sand dunes, grasslands, and woodlands are also present. The area is located in coastal plains that were once covered by seawater and that are now extensively used for irrigated rice cultivation. The climate is temperate and seasonal, with a mean of approximately 13°C during the coldest month (July) and approximately 23°C during the warmest month (January), but with a generally constant level of precipitation throughout the year (approximately 1300 mm average annual rainfall; Tassi et al. 2013). Overall, the water level of the entire hydrological system is regulated by rainfall and evaporation, which is more intense during summer when hydric deficit occurs. Water use for local rice irrigation is also more intense during spring/summer (Villanueva et al. 2000).

Capture and Sampling. We captured Snail Kites using a modified Verbail trap (Bloom et al. 2007), which consisted of four to six nylon filament, spring-mounted nooses placed along a wooden perch. The perch was placed in a bush or small tree known to be used as a snail extraction location used by several Snail Kites. We identified up to four such branches, where traps were then placed. Nooses of the trap were positioned along the length of the wood perch, such that when a Snail Kite landed on the perch, it released the spring and snared the Snail Kite's legs. The nooses were anchored to the trap with a rubber strap so as to prevent injury to the Snail Kite while trapped. We used up to three traps simultaneously (located <100 m from each other) and observed traps from kayaks at a distance of 80–100 m. Once a Snail Kite became trapped, we quickly approached by kayak, extracted the Snail Kite from the trap, placed it in a holding can, and returned to shore for processing (Hull and Bloom 2001).

Once on shore, we banded each Snail Kite using a numbered metal band provided by CEMAVE (Centro Nacional de Pesquisa e Conservação de Aves Silvestres, the Brazilian bird banding agency). Snail Kites were then classified as either juveniles or adults (i.e., at least 1 yr old) and sexed based on morphological characters (e.g., plumage coloration) or using molecular methods (i.e., polymerase chain reaction and identification of CHD genes) if we had genetic material from blood sampling and feather collection. We collected morphometric data (e.g., unflattened wing chord, tarsus, footpad, hallux, and tail length) following Hull and Bloom (2001). Body mass was measured to the nearest gram using a Pesola® spring scale. Finally, each Snail Kite was outfitted with an Argos doppler satellite transmitter (12 g, model GT-12GS, Geotrak, Inc., Apex, NC, USA) using a backpack harness (Meyburg and Fuller 2007) made of tubular Teflon™ ribbon (Bally Ribbon Mills, Bally, PA, USA). The combined mass of the harness and transmitter averaged 5.3 ± 0.5% (mean ± SD) of the mass of the Snail Kites on which they were deployed, which is similar to the suggested upper permissible limit of 5% (Cochran 1980, Barron et al. 2010). Transmitters were programmed to transmit with a duty cycle of 8 hr on and 36 hr off, which is a fairly typical duty cycle for this size of transmitter and represents a compromise between data acquisition and battery limitations. All data were automatically synced with and stored on the online data repository movebank.org (Movebank 2019).

Data Analysis. Prior to analyses, we applied the Douglas Argos-Filter (Douglas et al. 2012) within Movebank. We used the distance angle rate filter method, which retains points that fit a realistic rate of movement. We kept all location classes of "1" or higher, which correspond to an error radius of <1500 m, and set a maximum plausible movement speed (min.rate) of 100 km/hr to filter the remaining fixes. Lastly, we filtered the data for each individual to include only the first location in each hour. This data set was used for calculations of home range size. For analyses of migration statistics, we additionally applied the best-of-day filter, to select the highest quality and most representative data point for each duty cycle. This was done to minimize potential biases in calculation of distance and speed metrics associated with sampling rate and position accuracy (Rowcliffe et al. 2012), and to facilitate comparisons with future studies.

All further analyses were completed in R version 3.6.1 (R Core Team 2019). We created movement bursts for each individual, year, and season (here defined as austral fall [1 January–30 June] and spring [1 July–31 December]), which enabled us to capture movement patterns associated with seasonal migrations (Phipps et al. 2019). For each individual, we excluded data from incomplete seasons, resulting in 23 complete seasons from seven individuals, across 2 yr (2018–2019).

We calculated home ranges across the full annual cycle and extent of the tracking data for each individual using dynamic Brownian bridge movement models as developed in the *move* package (Kranstauber and Smolla 2020). The Brownian bridge movement model is based on a probabilistic model of movement between successive relocations, and is an improvement over classic home range metrics, such as kernel density and minimum convex polygons because it incorporates position accuracy and time between locations (Horne et al. 2007). Further, the dynamic Brownian bridge movement model, as applied here, incorporates a behavioral change point analysis in a sliding window along the movement path to distinguish between movement patterns (e.g., migration or stationary periods) and adjusts the probabilistic area of use between successive locations, which has been shown to increase predictive accuracy of the realized area of use (Kranstauber et al. 2012). To calculate home ranges, we set the grid cell size to a 10 × 10-km resolution, which provided relatively high-resolution mapping over the large geographic area of our study. The location error for each unique location was set as the Argos error radius (i.e., an error estimate provided by the Argos satellite system for each location in the raw data set). Based on recommendations of the package creators (Kranstauber et al. 2012), we set the window size and margin, which control the Brownian motion variance, at 31 and 11 locations, respectively; this should capture the variance in the biological rhythm of a raptor where daily movements are interspersed by nocturnal rest periods (e.g., Buechley et al. 2018b). We then identified the 50% and 95% home ranges for each individual. Further, to identify areas of concentrated use by multiple tracked individuals, we mapped the area of overlap of the 95% home ranges of all individuals.

We then calculated net-displacement of each burst (individual-year-season) using the *adehabitatLT* package (Calenge 2020). Migration start and end points were determined from visual inspection of net-displacement plots and movement trajectories (Phipps et al. 2019). Although all individuals relocated between different sites throughout the annual cycle, only four individuals migrated, as evidenced by regular to-and-from seasonal movements. For these four migrants, we identified the point at which an individual first initiated a migration (i.e., the first point at which net-displacement continuously increased away from the summer or winter range) and the end of migration (i.e., the first point at which net-displacement values plateaued upon reaching the winter or summer range; Phipps et al. 2019; Supplemental Material Fig. S1).

Migration parameters were computed over the duration of each full season, as well as for individual migration trajectories. We computed the following parameters using the *amt* package (Signer et al. 2019): (a) start and end dates (calendar and Julian days); (b) start and end latitudes and longitudes; (c) duration; (d) direct distance (Euclidean) between start and end points (km); (e) cumulative distance (sum of Euclidean distances along the full path between start and end points, km); (f) migration straightness (direct distance/cumulative distance); and (g) migration speed (cumulative distance/migration duration; Buechley et al. 2018a, Phipps et al. 2019). For complete migrations, we identified the number and duration of time at stopover sites, which we defined as two or more consecutive positions within a 15-km radius where an individual remained for at least 48 hr (Pedrana et al. 2018). Given that the transmitter's duty cycle was 8 hr on and 36 hr off, this definition necessitated that a location fix from at least two duty cycles occurred at a stopover. Nevertheless, the duration of most stopovers was much longer. The small number of tracked Snail Kites precluded inferential statistical analysis. Unless noted otherwise, all values represent means ± SD, combining data from 2018 and 2019.

RESULTS

We captured and tagged a total of 10 Snail Kites (2 females and 8 males). We aged all captured Snail Kites as adults, except one female (#78), for which we were not certain of age. We found several Snail Kite nests with eggs during the time we were capturing Snail Kites at Taim Ecological Station, although we found no definitive evidence that the Snail Kites we captured were breeding (e.g., none had a brood patch).

Individual Summaries. Of 10 transmitters deployed, seven transmitted at least one complete season after deployment and showed that most Snail Kites initially moved toward the northwest, entering the Paraguay-Paraná River Basin and thereafter moving northward along the basin through northeastern Argentina (Fig. 1). Two Snail Kites, both females (#47 and #78), continued moving north through Paraguay, the Pantanal, and central Brazil (along the Araguaia-Tocantins River Basin) as far as the mouth of the Amazon River, where they overwintered for several months in the states of Pará and Amapá (south and north of the mouth of the Amazon River, respectively), although the latter only did so in 2018 (Fig. 1, 2, S2). Two other Snail Kites (#48 and #80) followed a similar route through Paraguay, then moved northwest into Bolivia through the Chaco ecoregion, reaching the basin of the Mamoré River in northern Bolivia, where they overwintered in 2018 (Fig. 1). Only one of those Snail Kites (#80) returned to overwinter in Bolivia in 2019, although at a location further south than the one it occupied in 2018, and where it stopped transmitting (Fig. 1, 2, S2). Three other Snail Kites (#50, #79, and #82) remained year-round in the vicinity of southern Brazil, Uruguay, northeastern Argentina, and Paraguay (Fig. 1). Two Snail Kites (#47 and #50) returned to the vicinity of the capture site (i.e., <150 km) in subsequent breeding seasons (2018 and 2019), although whether they attempted to breed is unknown.

Three tags did not transmit through a full season. One (#49) transmitted for approximately 2 mo, during which time the Snail Kite moved northwest into Argentina and Paraguay, re-entered Brazil, and then experienced an abrupt termination in data transmission while in the state of São Paulo. Another (#81) transmitted for approximately 5 mo, during which time the Snail Kite initially moved northwest through Argentina, then northward through central Paraguay, re-entering Brazil and crossing the Pantanal region, then experiencing an abrupt termination of transmission in the state of Mato Grosso. Another (#77) sent intermittent fixes over <9 mo, including an approximately 5-mo gap in transmission during which time the Snail Kite moved into the state of Mato Grosso, Brazil; the transmitter then began sending static transmissions indicating mortality or a dropped transmitter**.** As a result, we did not analyze the data from these three tags.

Variation in Full Season Movements. Mean direct distance between the breeding site and nonbreeding sites was similar between seasons (1643 km in fall vs. 1528 km in spring); however, cumulative movement distance was >1000 km longer in spring than in fall (Table 1), likely due to greater tortuosity in the movement path in spring vs. fall (see variable "Straightness" in Table 1) and because of one Snail Kite (#47), which moved a cumulative distance of >4000 km during two spring seasons (Table 1, Fig. 3). Full season migration speed was higher in spring (19 km/d) vs. fall (13 km/d), with a similar level of variation between seasons (Table 1, Fig. 3). In spite of the variation in movement patterns among Snail Kites, there was a clear trend for Snail Kites to be located at more northerly latitudes during austral winter, as well as a slightly more easterly position during winter (Fig. S3). Notably, both Snail Kites that migrated the longest distance (#47 and #78) and overwintered at the mouth of the Amazon River were the only two females that we tracked. These two Snail Kites also exhibited generally higher straightness in movements and faster migration speeds in fall than males (Table 1).

Variation in Movements Between Years. We were able to collect more than one year of data for five Snail Kites whose seasonal movement patterns were generally similar between years. Notable exceptions are the cumulative and direct fall movement distance for one female Snail Kite (#78), which migrated to the mouth of the Amazon River in 2018, but not 2019, and therefore exhibited notably higher movement values in both fall and spring of 2018 than in 2019. Another Snail Kite (#82) moved over twice the direct distance in fall 2019 than in 2018, whereas in spring it moved over three times as far in 2018 than in 2019 (Table 1). Nevertheless, that Snail Kite remained in the vicinity of southern Brazil, Uruguay, northeastern Argentina, and Paraguay during both years (Fig. 1).

Some Snail Kites exhibited substantial interannual variation in migration patterns. Snail Kite #48 migrated to northern Bolivia in 2018, but not in 2019 (Fig. 1, 2). Snail Kite #78 overwintered at the

Figure 1. Overview map of full season movements of individual Snail Kites (*Rostrhamus sociabilis*) in South America during 2018–2019. Brazilian state abbreviations are: Amazonas (AM), Amapá (AP), Goiás (GO), Mato Grosso do Sul (MS), Mato Grosso (MT), Pará (PA), Paraná (PR), Rio Grande do Sul (RS), São Paulo (SP), Tocantins (TO). Map created in Quantum GIS, using Google imagery.

mouth of the Amazon River in 2018, but remained near the border of Paraguay and Argentina in 2019 (Fig. 1, 2, S2). Additionally, Snail Kite #80 exhibited a direct fall migration distance of >1000 km longer in 2018 than in 2019 (Table 2). This individual also exhibited less than half the fall migration speed (with stopovers) in 2018 than in 2019 (Table 2), since it spent much more time on stopover during fall migration in 2018 vs. 2019 (i.e., 93 vs. 13 d, respectively; Table 3).

Seasonal Variation in Migration and Stopovers. The months of peak migration activity were February–June (i.e., fall migration) and September–October (spring migration; Fig. S3). Fall migration began as early as 7 January (mean Julian start date: 48 ± 38.0), and ended as late as mid-June (mean

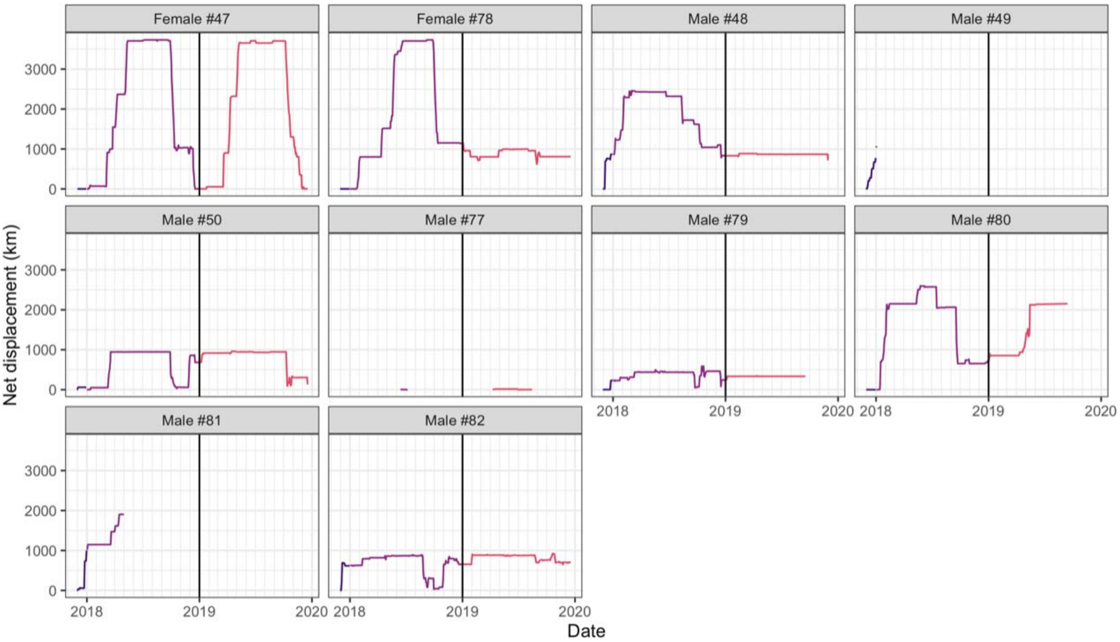

Figure 2. Net displacement over time of individual Snail Kites (*Rostrhamus sociabilis*) for each fall and spring full season in South America during 2018–2019.

Julian end date: 130 ± 35.3; Table 2). Spring migration began as early as 15 July (mean Julian start date: 249 ± 37.2) and ended as late as mid-December (mean Julian end date: 318 ± 39.4; Table 2). Mean total duration of fall migration (82 d) was longer than that of spring migration (69 d), with a similar level of variation in both seasons (45.4 vs. 40.7 d, respectively; Table 2). A similar pattern was evident in the duration of migration without stopover days included (Table 2). Snail Kites used up to five stopover sites during migration, with a mean of three stopovers in fall and two in spring (Table 3). Mean time spent on stopover was 56 d in fall and 48 d in spring (Table 3), representing 68% and 70% of the total duration of fall and spring migration, respectively (Table 2). Although the variable duty cycle of transmitters could marginally affect calculations of stopover durations, we expect this to be minimal given the relatively long duration of time spent at most stopovers (Table 3).

Average straightness of migration was similar between seasons, as was cumulative and direct distance of migration (Table 2). Average migration speed with and without time at stopovers included were both higher in spring vs. fall, and showed similar levels of variation between seasons (Table 2).

Seasonal Home Range Parameters. The area of overlap of the home ranges of the seven Snail Kites that were tracked for at least one full season showed highly used areas, especially in northeastern Argentina, southern Paraguay, and the capture site (Fig. 4). Outside of this region are home ranges of two male Snail Kites that used sites in northern Bolivia (#48 and #80) and of two females in northeastern Brazil at the mouth of the Amazon River (#47 and #78; Fig. 4). Full season mean 50% home range size was 2329.0 ± 2493.1 km^2, and the mean 95% home range was 137,386.0 ± 139,391.2 km^2.

DISCUSSION

Overall, the Snail Kites we tracked from a breeding site in the coastal plains of southern Brazil exhibited high variation in movement timing, rates, and routes, with some migrating between two well-defined sites, and others exhibiting nomadic/facultative movements. Notably, the two Snail Kites that migrated the farthest distance were the only two females we tracked. These results provide the first evidence that individual Snail Kites undertake both short- and long-distance movements in South America, with some utilizing major wetland areas such as the Pantanal, and multiple river basins such

Table 1. Individual movement histories of Snail Kites (*Rostrhamus sociabilis*) during full Fall (defined as 1 January–30 June) and Spring (1 July–31 December) seasons in South America. Most Snail Kites had two years of data. All Snail Kites were adults (i.e., at least 1 yr old), except #78, whose age we were not able to determine.

SEASON	ID	YEAR OF DATA	SEX	YEAR	STRAIGHTNESS	CUMULATIVE DISTANCE (km)	DIRECT DISTANCE (km)	SPEED (km/d)
Fall season (1 Jan–30 Jun)								
	47	1st	F	2018	0.84	4402	3716	24
	47	2nd	F	2019	0.84	4437	3708	25
	78	1st	F	2018	0.86	4320	3703	24
	78	2nd	F	2019	0.11	1501	163	8
	48	only	M	2018	0.60	2426	1455	13
	50	1st	M	2018	0.68	1386	942	8
	50	2nd	M	2019	0.44	1096	484	6
	79	only	M	2018	0.28	905	253	5
	80	1st	M	2018	0.80	3206	2570	18
	80	2nd	M	2019	0.71	2643	1888	17
	82	1st	M	2018	0.27	936	252	5
	82	2nd	M	2019	0.58	1004	583	6
Mean ± SD					**0.6 ± 0.26**	**2355 ± 1427**	**1643 ± 1439**	**13 ± 8.0**
Spring season (1 Jul–31 Dec)								
	47	1st	F	2018	0.65	5710	3705	31
	47	2nd	F	2019	0.74	4974	3703	29
	78	1st	F	2018	0.93	2963	2768	16
	78	2nd	F	2019	0.18	1268	232	8
	48	only	M	2018	0.64	2529	1629	14
	50	1st	M	2018	0.13	3720	501	20
	50	2nd	M	2019	0.47	1989	934	12
	79	only	M	2018	0.06	3823	224	22
	80	only	M	2018	0.68	3430	2328	19
	82	1st	M	2018	0.14	4471	609	26
	82	2nd	M	2019	0.09	2077	179	12
Mean ± SD					**0.4 ± 0.32**	**3359 ± 1359**	**1528 ± 1382**	**19 ± 7.6**

as the Amazon, Araguaia-Tocantins, Paraná-Paraguay, and Mamoré, within the same year. The differences in the extent of individual movements within and between years agree with the highly variable seasonal and yearly abundance of Snail Kites observed in the southern portions of their range (i.e., Uruguay, Argentina and Rio Grande do Sul, Brazil; Arballo and Cravino 1999, Bencke 2001, Juhant 2010, Zilio et al. 2014).

Mean seasonal movement distances of >1500 km that we detected stand in stark contrast to those of Snail Kites in Florida, which move much shorter distances (i.e., on the order of hundreds of km) between wetlands across much of the state (Martin et al. 2006, Reichert et al. 2016). In North America, large wetland ecosystems such as the Everglades are not available to Snail Kites outside of the Florida Peninsula, whereas in South America large wetlands occur across the vast lowlands of the continent. Long-distance movements in South America therefore allow Snail Kites access to seasonally available resources across a much larger spatial scale than what is available to Snail Kites in Florida.

In South America, Snail Kites are seen in the Pantanal wetlands of southwestern Brazil from April to October (Cintra and Yamashita 1990), and our results support the hypothesis put forth by Antas (1994) that those Snail Kites are likely breeders from Argentina, Uruguay, or the state of Rio Grande do Sul, Brazil. That they did not migrate along the Atlantic coast is notable, given that movements of large flocks of Snail Kites are seen along the coast (A. Jahn unpubl. data). Such movements may represent Snail Kites that both breed and overwinter along the coast. Additionally, movements we documented between the coastal wetlands where we captured Snail Kites and wetlands along the Paraná-Paraguay River are similar to movements of other wetland bird

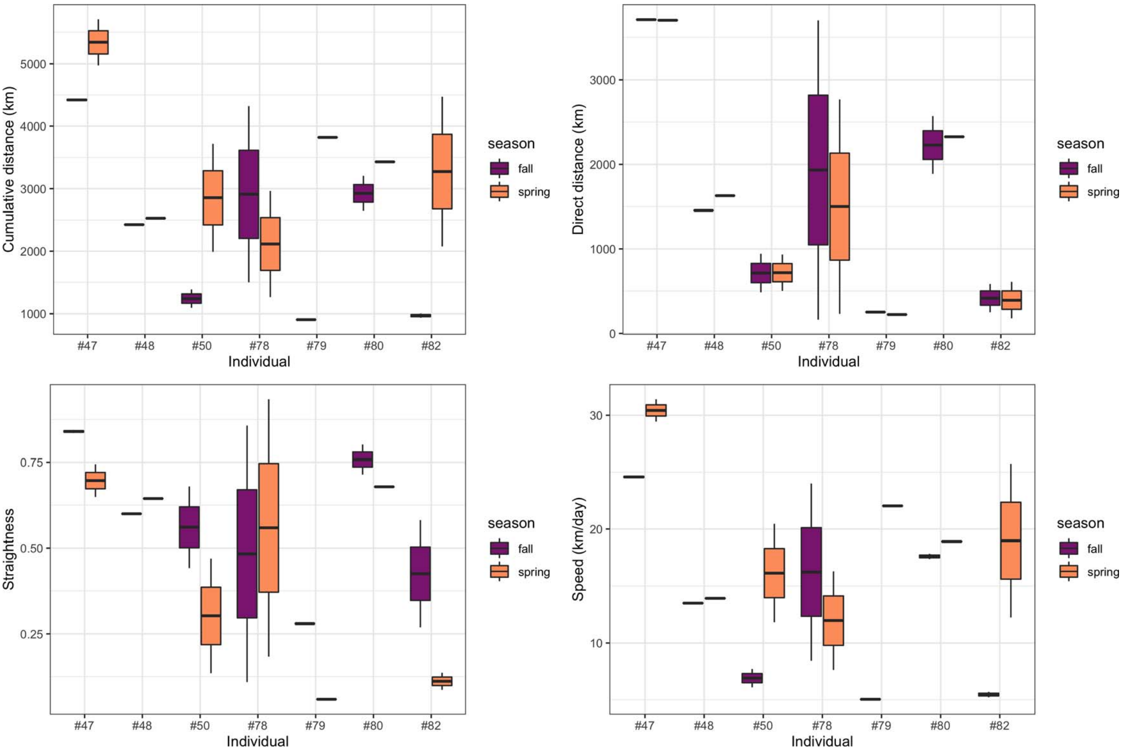

Figure 3. Full season movement histories of Snail Kites (*Rostrhamus sociabilis*) in South America during 2018–2019.

species in the region, such as the Rosy-billed Pochard (*Netta peposaca*; Olrog 1968, Belton 1984), Neotropical Cormorant (*Phalacrocorax brasilianus*; Olrog 1975), and Coscoroba Swan (*Coscoroba coscoroba*; Calabuig et al. 2010), raising the possibility of even more widespread movements in this region by large numbers of wetland species.

Because Snail Kites feed almost exclusively on snails, movements of Snail Kites throughout the year likely track environmental conditions that maximize access to their primary food source. That freshwater snail abundance can be highly variable across space and time (Darby et al. 2006) may in large part explain the high variation in movements we detected. One proxy for snail availability could be water level, which other waterbirds such as Wood Storks (*Mycteria americana*) are also known to track (del Lama et al. 2015). The high variation in movements we detected is also typical of Snail Kites in Florida, where Snail Kite movements outside of the breeding season can be highly erratic and vary across sites (Reichert et al. 2016, Robertson et al. 2018) and among individuals (Valle et al. 2017). Indeed, Snail Kites in Florida move in response to food shortages associated with low water (Takekawa and Beissinger 1989, Beissinger 1995), and exhibit exploratory behavior in times of higher water levels and potentially higher food availability (Bennetts and Kitchens 2000). It has been shown that they change their movement rates to and from sites based on the availability of their snail prey (Cattau et al. 2016). Finally, Snail Kite movements in Florida also vary according to age, with dispersing Snail Kites being more likely to nest in habitats that are similar to where they were hatched (Fletcher et al. 2015). Thus, given what is known about how Snail Kites in Florida respond to water levels, the movement patterns we detected are likely a response to various drivers related to seasonal changes in water level and food abundance.

Rainfall and flooding predominated at our study site into early 2018; however, much less rain fell there in the second half of the year, and there was much more floating vegetation there in 2018 than in 2017 (L. Bugoni unpubl. data). Given that snails can be difficult to detect, excessive vegetative cover may

Table 2. Individual movement histories of Snail Kites (*Rostrhamus sociabilis*) in South America during migration only. Two Snail Kites had two years of data. All Snail Kites were adults (i.e., at least 1 yr old), except #78, whose age we were not able to determine.

SEASON	ID	SEX	YEAR	START DATE	END DATE	TOTAL DURATION (d)	DURATION WITHOUT STOPOVERS (d)	STRAIGHTNESS	CUMULATIVE DISTANCE (km)	DIRECT DISTANCE (km)	SPEED WITH STOPOVERS (km/d)	SPEED WITHOUT STOPOVERS (km/d)
Fall season (7 Jan–19 Jun)												
	47	F	1st	6 Mar	13 May	68	21	0.89	3687	3292	54	176
	47	F	2nd	19 Mar	10 May	52	19	0.91	4070	3689	78	214
	78	F	only	25 Jan	19 Jun	145	37	0.87	4128	3574	28	112
	48	M	only	7 Jan	5 Mar	57	18	0.72	2041	1478	36	113
	80	M	1st	13 Jan	25 May	132	39	0.83	3116	2601	24	80
	80	M	2nd	9 Apr	15 May	36	23	0.70	1979	1383	55	86
Mean ± SD						**82 ± 45.4**	**26 ± 9.3**	**0.8 ± 0.09**	**3170 ± 968.7**	**2670 ± 1031.9**	**46 ± 20.5**	**130 ± 53.3**
Spring season (15 Jul–18 Dec)												
	47	F	1st	30 Sep	18 Dec	79	25	0.66	5282	3481	67	211
	47	F	2nd	9 Oct	29 Nov	51	30	0.83	3986	3311	78	133
	78	F	only	26 Sep	14 Oct	18	18	0.98	2841	2788	158	158
	48	M	only	11 Aug	18 Dec	129	24	0.68	2407	1629	19	100
	80	M	only	15 Jul	23 Sep	70	8	0.94	2570	2407	37	321
Mean ± SD						**69 ± 40.7**	**21 ± 8.4**	**0.8 ± 0.15**	**3417 ± 1211.4**	**2723 ± 745.3**	**72 ± 53.7**	**185 ± 86.4**

Table 3. Number of stopovers and stopover duration (in d) of Snail Kites (*Rostrhamus sociabilis*) in South America during migration. Two Snail Kites had two years of data. All Snail Kites were adults (i.e., at least 1 yr old), except #78, whose age we were not able to determine.

SEASON	ID	SEX	YEAR	NO. STOPOVERS	TOTAL STOPOVER DURATION (d)	DURATION STOPOVER 1 (d)	DURATION STOPOVER 2 (d)	DURATION STOPOVER 3 (d)	DURATION STOPOVER 4 (d)	DURATION STOPOVER 5 (d)
Fall season (7 Jan–19 Jun)										
	47	F	1st	4	47	6	9	8	24	–
	47	F	2nd	2	33	13	20	–	–	–
	78	F	only	4	108	68	26	6	8	–
	48	M	only	3	39	13	3	23	–	–
	80	M	1st	1	93	87	6	–	–	–
	80	M	2nd	2	13	10	3	–	–	–
Mean ± SD				**3 ± 1.2**	**56 ± 36.9**	**33 ± 35.2**	**11 ± 9.6**	**12 ± 9.3**	**16 ± 11.3**	–
Spring season (15 July–18 Dec)										
	47	F	1st	2	54	44	10	–	–	–
	47	F	2nd	3	21	9	6	6	–	–
	78	F	only	0	0	0	–	–	–	–
	48	M	only	5	105	32	9	3	50	11
	80	M	only	1	62	62	–	–	–	–
Mean ± SD				**2 ± 1.9**	**48 ± 40.4**	**29 ± 25.3**	**8 ± 2.1**	**5 ± 2.1**	–	–

inhibit foraging performance (Bergmann et al. 2013), which may explain the smaller numbers of tracked Snail Kites that returned to the study site in 2018. Furthermore, Snail Kites can be locally absent during prolonged droughts in northern Argentina (Contreras et al. 1990, Di Giacomo and Krapovickas 2005), an observation that agrees with our finding that some individuals moved more in one year than others and that suggests a promising direction for future research into the proximate drivers of kite movements.

That the Snail Kites we tracked spent a mean 68% of the duration of fall migration and 70% of spring migration at stopover sites suggests that they are highly dependent on such sites for refueling and resting. Furthermore, that they moved at faster speeds and used fewer stopovers in spring vs. fall may be a result of competition for breeding territories, nest sites, and/or mates (McNamara et al. 1998). Snail Kites in Florida experience higher mortality during periods of low water (Martin et al. 2006), suggesting that if the stopover sites Snail Kites use in South America were to experience drought, large numbers of Snail Kites could be affected. Notably, two of the Snail Kites we tracked crossed the Chaco ecoregion, where little to no water may be found for hundreds of kilometers, which underscores the need to better understand how kites use stopover sites before and after crossing such a barrier.

Implications for Wetland Conservation. Wetlands across the planet are facing numerous threats, such as draining for agriculture, urbanization, invasive species, pollution, and climate change, all of which threaten their integrity and function. Because wetlands provide vital ecosystem services for both wildlife and humans, and harbor high levels of biodiversity, there is an urgent need to understand how to best conserve these unique ecosystems and the species that rely on them. However, developing effective conservation plans to protect these systems first requires an intimate understanding of how they function and how increasing human-related pressures are impacting their integrity. An effective way of doing so is by monitoring a specific set of wetland species characterized by a set of traits that make them ideal indicators of ecosystem change, which has been done using the Snail Kite as an indicator in Florida (DeAngelis et al. 1998). Due to their strict dependence on wetland habitat and their position near the top of the food web, many obligate wetland birds are highly sensitive to change, making them sentinels of impacts on wetland dynamics (Amat and Green 2010). A more detailed understanding of the

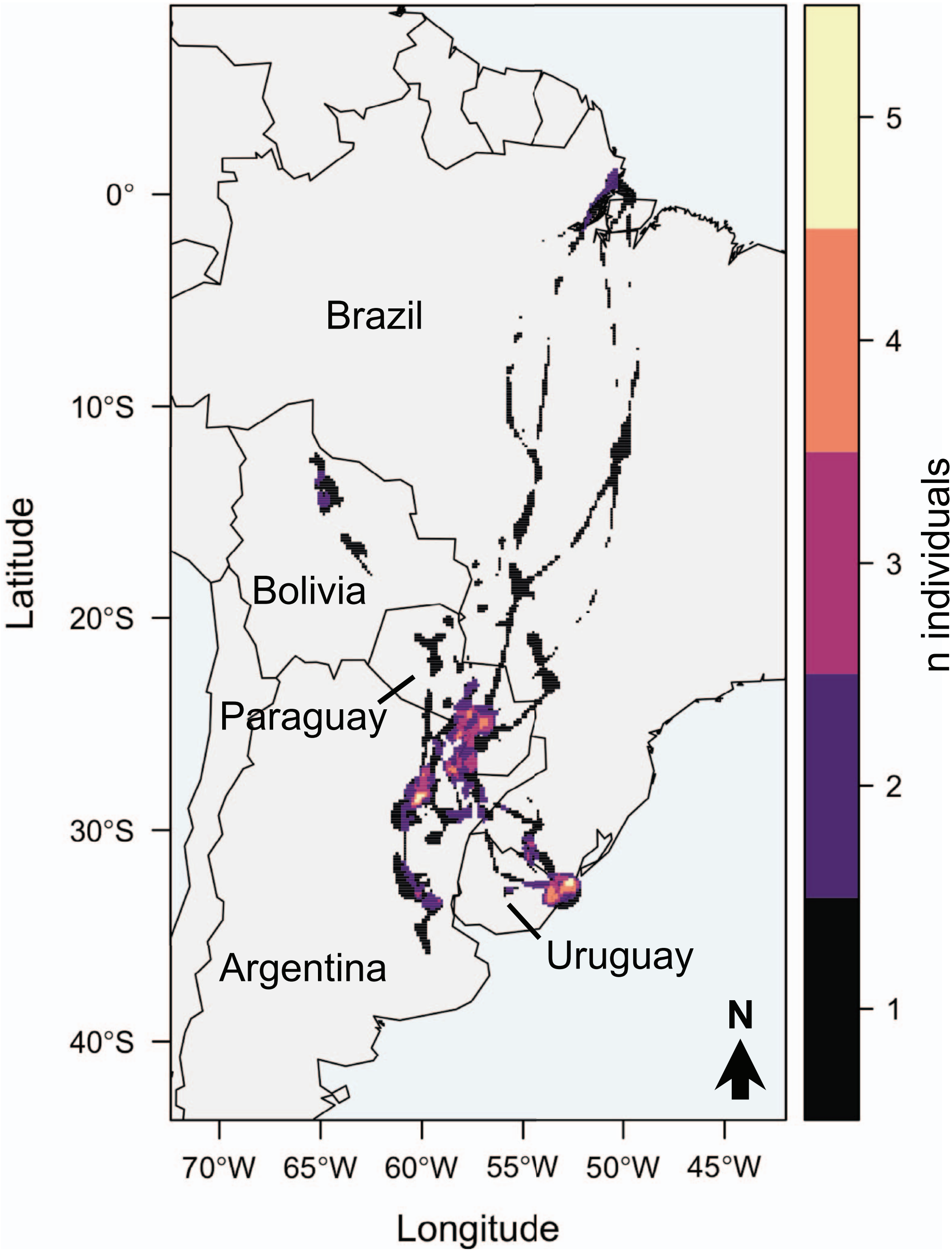

Figure 4. Area of overlap of 95% home ranges of seven Snail Kites (*Rostrhamus sociabilis*) in South America during 2018–2019, as calculated by dynamic Brownian bridge movement models. See online version for interpretation of color.

full annual cycle of Snail Kites in South America could lead to their use as sentinels across the various wetland ecosystems they use throughout their range.

Understanding how wetland birds are responding to current changes also provides vital information necessary to develop effective conservation and management efforts to conserve their populations over the long term. A long-term, multi-national effort to monitor Snail Kites and other obligate wetland birds across South America has the potential to inform natural resource management programs at wetland sites heavily used by this and other species. Given that the Paraná-Paraguay River watershed is shared among Argentina, Bolivia, Brazil, Paraguay, and Uruguay, Snail Kite monitoring efforts among these countries could, over the long-term, yield novel insights into the health of that important watershed.

Nevertheless, due to their tendency to move large distances both within and between seasons, wetland birds such as Snail Kites face different threats throughout the year. Given the extensive conversion of native habitat to industrial agriculture on their breeding grounds (e.g., rice cultivation in southern Brazil), exposure to pesticides or drought could be the primary risk to Snail Kite survival during the breeding season, whereas habitat destruction may be the most important threat during migration and winter. Additional mortality could occur through collision with wind energy facilities, as several large wind farms have been recently established near coastal wetlands in southern Brazil. Snail Kites' breeding success can also be negatively impacted by low water levels (Dreitz et al. 2001, Beissinger and Snyder 2002). Thus, a comprehensive evaluation of the drivers of the population dynamics of this unique species requires research that focuses on both intrinsic (e.g., demographics, energetics) and extrinsic (e.g., water levels, food availability) drivers throughout the year. Additionally, future studies could test the hypothesis that Snail Kites track environmental conditions that maximize their access to snails throughout the year, including the use of artificial reservoirs (Repenning et al. 2010). In particular, spring may be a key time of year for migratory Snail Kites because their higher migration speeds in spring vs. fall may be due to the need to arrive on breeding grounds in a timely manner, as is true of numerous migratory bird species (Nilsson et al. 2013).

In conclusion, we provide the first evidence of highly variable movements of South American Snail Kites, which exhibit both short- and long-distance movements, movements across significant barriers (e.g., the arid Chaco ecoregion), and highly variable routes, home ranges, and movement phenology between years. Snail Kites in South America likely fall along a continuum between nomadism and true migration, which may vary across populations and between years for a given individual, and for which mechanistic models exist (Mueller and Fagan 2008, Jonzén et al. 2011). Because the breeding colony of Snail Kites at Taim Ecological Station represents one of the largest known breeding colonies of the species in southern Brazil, it is likely that the movement patterns we detected characterize those for breeding populations of this species across southern Brazil. Because the two Snail Kites that moved the longest distance in our study were both females, future studies on movement in this species, at least in South America, should include research into possible sex-dependent drivers of movement. Given the highly variable nature of their movements, future studies are needed to elucidate the drivers of such variability, which could help determine the time of year that is most limiting in terms of survival (Klaassen et al. 2014, Rushing et al. 2017), which in turn depends on understanding the full annual cycle (Marra et al. 2015). Furthermore, given the highly variable movements among individuals and between years, research on Snail Kite movements across their range offers an opportunity to further elucidate the balance between ultimate and proximate drivers of movement generally. This type of research requires information on such mechanisms as carry-over effects and migratory connectivity (Rushing et al. 2016), including the relationship between dispersal and reproductive success (Robertson et al. 2018), which would lend key insights into Snail Kites' potential to adapt to the rapid changes occurring throughout their range.

SUPPLEMENTAL MATERIAL (available online). Figure S1: Example of a manual migration delineation for one individual Snail Kite (*Rostrhamus sociabilis*) based on net displacement over time. Figure S2: Net displacement of individual Snail Kites (*Rostrhamus sociabilis*). Figure S3: Boxplots of latitude and longitude of Snail Kites (*Rostrhamus sociabilis*), by month, during 2018–2019.

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