Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

ARTICLE

Rainy cycles in South America as a driver for the breeding of the Black Skimmer (*Rynchops niger*) and the Large-billed Tern (*Phaetusa simplex*) (Aves, Charadriiformes)

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Abstract. The Black Skimmer (*Rynchops niger*) and the Large-billed Tern (*Phaetusa simplex*) are two migratory waterbirds that breed simultaneously on many river beaches in South America. Both are polytypic taxa with little information about the distribution and nonbreeding ("wintering") areas. Based on data from the literature, citizen science websites, fieldwork, and specimens housed in natural history museums, we revised the distribution of some of the main breeding colonies in South America, comparing it with continental rainy cycles to identify generalities about the role of precipitation seasonality on the defining intratropical migration routes of these species. Our data suggest that the seasonal precipitation cycle of South America directly influences the reproductive timing and distribution of both species, which is largely circumscribed by South America's rivers. After breeding on sandy beaches during the dry season, both species disperse in small groups or even individually – not in large flocks as seen in breeding areas – making it difficult to find general migration patterns during the rainy season. Nonetheless, individuals of both species tend to follow the course of the largest rivers of the continent and even alternative routes to disperse into several areas throughout South America during the nonbreeding season.

Keywords. Biogeography; Waterbirds; South American rivers; Migration; *Rynchops; Phaetusa.*

INTRODUCTION

The Black Skimmer (*Rynchops niger*) and the Large-billed Tern (*Phaetusa simplex*) are migratory waterbirds found throughout South America. Currently, *Rynchops niger* has three accepted subspecies: *R. n. niger,* found in North and Central Americas, and *R. n. cinerascens* and *R. n. intercedens,* which occur in South America, where *Phaetusa simplex simplex* and *P. s. chloropoda* are mostly found (Gochfeld & Burger, 1996; Gochfeld *et al.,* 2018; Gouvêa, 2018). Despite the considerable number of Neotropical and Nearctic migrants that use a variety of South American (SA) habitats, information about the migration patterns in this region is still scant for many species (Faaborg *et al.,* 2010; Somenzari *et al.,* 2018; Jahn *et al.,* 2020). Intratropical movements are poorly known for waterbirds and their seasonal occurrence in many important wetland regions remains poorly known (Antas, 1994; Stotz *et al.,* 1996; Chesser, 2010; Antas *et al.,* 2016; Somenzari *et al.,* 2018; Jahn *et al.,* 2020).

There is abundant information about the biology of the nominate form of the Black Skimmer (*R. n. niger*). On the other hand, the SA populations of Black Skimmers and Large-billed Terns are good examples of the scarcity of studies about migratory South American waterbirds (Zusi, 1996; Sick, 1997; Faaborg *et al.,* 2010; Rappole,

Pap. Avulsos Zool., 2023; v.63: e202363028
https://doi.org/10.11606/1807-0205/2023.63.028
https://www.revistas.usp.br/paz
https://www.scielo.br/paz
Edited by: Carlos José Einicker Lamas
Received: 23/09/2022
Accepted: 13/07/2023
Published: 01/09/2023

ISSN On-Line: 1807-0205
ISSN Printed: 0031-1049
ISNI: 0000-0004-0384-1825

2013; Davenport *et al.,* 2016; Somenzari *et al.,* 2018). *Rynchops n. niger* breeds mostly in coastal regions and islands of the USA and Mexico, with scattered colonies in Central America and northern South America, whereas *R. n. cinerascens, R. n. intercedens,* and *P. simplex* spp. breed in sand beaches mostly along the largest SA rivers. However, the breeding cycle and even the distribution of the SA skimmers and terns, including their migration routes, are still inaccurate, with divergences in the literature and major gaps in the natural history of these populations (Gochfeld & Burger, 1996; Zusi, 1996; Sick, 1997; Livezey & Zusi, 2007; Antas *et al.,* 2016; Davenport *et al.,* 2016; Vieira *et al.,* 2018). It is assumed that breeding season in parts of South America takes place between April and November, following the dry season on the great rivers, although precise dates may vary by location and from year to year, depending on the end of the rainy season at the headwaters (Gochfeld & Burger, 1996; Zusi, 1996; Antas *et al.,* 2016; Gouvêa, 2018).

In South America, Black Skimmers and Large-billed Terns have a wide distribution and mainly occur in lower densities out of the breeding season. Estimates of their population sizes are inaccurate and current depictions of their distribution maps are somewhat coarse. Also, their nonbreeding sites remain poorly known (Harrison, 1985; Gochfeld & Burger, 1996; Gouvêa, 2018). The lack of accurate distribution ranges and population estimates, as well as published data on the threats to the populations, complicates assessments regarding their vulnerability. Currently, both species are classified as of Least Concern (LC) IUCN (2018) but the current status may not represent their real situation (Lambertucci *et al.,* 2014). Nevertheless, it is undeniable that their habitats and feeding resources are likely threatened due to overfishing, climate change (affecting the flood and drought seasonal cycles), and degradation pressures, whether through mining, deforestation, hydroelectric construction, and river damming, which regulate the river cycles and prevent the formation of sand beaches, directly affecting the breeding habitats of these birds (Gochfeld, 1979; Burger & Gochfeld, 1994, 1996; Zusi, 1996; Antas *et al.,* 2016; IUCN, 2018). All these factors are causes of concern and directly contribute to the observed population decline in many sites (Tyler, 2004; Gopi *et al.,* 2006; Demey *et al.,* 2007; Das, 2015; Dilawar & Sharma, 2016; IUCN, 2018; Gouvêa, 2018).

Here, we rely on vouchered museum specimens and thousands of verifiable photographs from publicly available repositories to describe general distributional patterns of South American populations of *R. niger* and *P. simplex*. Specifically, we assess the association between distributional patterns and precipitation seasonality and map the breeding and nonbreeding ("wintering") areas of these two species, with a particular focus on Brazil.

MATERIAL AND METHODS

Our dataset was composed of 882 (*R. niger:* 530; *P. simplex:* 352) vouchered museum specimens from 13 ornithological collections (Table 1 and Supplementary Material), literature information, our fieldwork, and thousands of reliable, personally checked data from the website WikiAves (*R. niger:* 3,200 and *P. simplex:* 2,902 photographs (Wikiaves, 2017) and eBird data (*R. niger:* 65,536 and *P. simplex:* 15,366; photographs and lists; Sullivan *et al.,* 2009). To map the geographic distribution of each taxon within these two species, we distinguished, when available in specimen labels or photograph descriptions, breeding from nonbreeding sites. Fieldwork was performed by LFS and ACG on a yearly basis between 2005 and 2022 at various breeding sites throughout Brazil (see Supplementary material). The distribution of each taxon over time was mapped using QGIS 2.4.0. Climate data (temperature and precipitation) were based on Reboita *et al.* (2010) and Matsuura (2017), who presented a compilation of data collected between 1980 and 2009.

Table 1. Number of specimens of Black Skimmer *(Rynchops niger)* and Large-billed Tern *(Phaetusa simplex)* examined in the ornithological collections.

Museum Collection	*R. niger*	*P. simplex*
BNHM (Natural History Museum, Tring, UK)	68	0
COP (Coleccíon Ornitologica Phelps, Caracas, Venezuela)	12	20
EBRG (Estación Biologica Rancho Grande, Maracay, Venezuela)	5	5
IAvH (Instituto Alexander von Humboldt, Villa de Leyva, Colombia)	5	5
ICN (Instituto de Ciencias Naturales, Bogotá, Colombia)	12	15
MNRJ (Museu Nacional, Rio de Janeiro, Brazil)	14	19
MOFURG (Museu Oceanográfico da Universidade Federal do Rio Grande, Rio Grande, Brazil)	7	0
MPEG (Museu Paraense Emílio Goeldi, Belém, Brazil)	11	27
MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil)	79	119
AMNH (American Museum of Natural History, New York, USA)	173	117
MCZ (Harvard University Museum of Comparative Zoology, Cambridge, USA)	142	25
NRM (Naturhistoríska Riksmuseet, Stockholm, Sweden)	1	0
ZSM (Zoologische Staatssammlung Munich, Munich, Germany)	1	0

RESULTS

In South America, *P. simplex* (Fig. 1) and *R. niger* (Figs. 2A, 2B) exhibit broadly overlapping distributions and usually share the same breeding sites. Nesting colonies of both species are found during the dry season when sandy beaches along rivers are fully exposed. On the other hand, the preferred breeding sites of the nominate form of *R. niger* are isolated sites, such as coastal islands, beaches, or dead vegetation deposited in barrier islands and mangroves (Zusi, 1996; Sick, 1997; Das, 2015), but man-made structures such as dredged material islands (Mallach & Leberg, 1999) and flat roofs (Coburn *et al.,* 2001) have also been reported. In South America, we identified four main breeding areas (Fig. 3), corresponding roughly to the largest river basins in the continent. *Phaetusa simplex* was found breeding in all four areas, whereas *R. n. cinerascens* was found only in the Amazon/Orinoco breeding area, and *R. n. intercedens* in the other three.

The northern breeding site corresponds with the Amazon and Orinoco river basins, covering their

Figure 1. Distribution of Large-billed Tern *(Phaetusa simplex)* based on fieldwork, literature, museums and digital records.

major rivers and tributaries, such as Trombetas, Tapajós, Madeira, and Purús. The breeding season occurs from July to December, with a peak in September. In northern South America (Venezuela, Guyana, and Colombia), the breeding season may start in mid-October and last until February, with scarce records into April. The second breeding site corresponds to the Tocantins and Araguaia river basin, located mainly in the Cerrado and the Amazon-Cerrado ecotone. The breeding season begins and ends earlier, lasting from June to October.

The third breeding zone comprises the Paraguay River basin, located mainly in the Pantanal and Cerrado biomes. It covers the Paraguai, Cuiabá, Negro, Taquari, and Miranda rivers, spreading from the Brazilian states of Mato Grosso and Mato Grosso do Sul and including adjacent Paraguay and Bolivia. As in the Amazon/Orinoco, the breeding season takes place from July to December, with birds starting to aggregate in colonies in May. The last and smallest breeding zone corresponds to the lower Paraná River in Argentina, the Uruguay River basin in Argentina, Uruguay, and the southernmost portion of Brazil, including its tributaries the Ibicuí and Jacuí rivers, in the state of Rio Grande do Sul. In this region, the breeding season begins later, from October to January and early February.

The breeding of *R. n. cinerascens, R. n. intercedens, P. s. simplex,* and *P. simplex chloropoda* is closely linked to the lowest precipitation season in the lowlands of South America (Figs. 4A, 4B), where the sandbanks of main rivers are exposed during the seasonal drought, providing suitable nesting sites. June is within the rainy season of the Northern Hemisphere portion of South America, while in most of the continent May to September is

Figure 2A. Distribution of Black Skimmer *(Rynchops niger)* based on fieldwork, literature, museums and digital records.

Figure 2B. Distribution map of Black Skimmer *(Rynchops niger)* based on 530 skins distributed in 13 ornithological collections: (68) BNMN; (12) COP; (5) EBRG; (5) IAVH; (12) ICN; (14) MNRJ; (7) MOFURG; (11) MPEG; (79) MZUSP; (173) AMNH; (142) MCZ, (1) ZSM e (1) NRM.

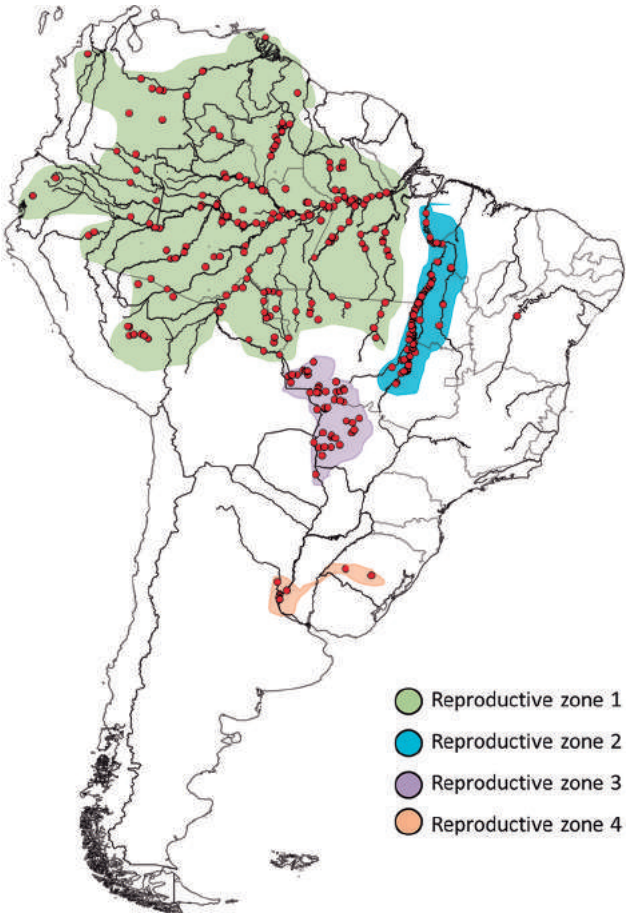

Figure 3. The four major breeding zones in South America: *Rynchops niger cinerascens* is present only in zone 1, while *R. n. intercedens* is present in zones 2, 3, and 4; *Phaetusa simplex* is present in all breeding zones and it also has a record of reproductive activity in the São Francisco River in Bahia (from August-September 2014) (Wikiaves, 2017) and in Trinidad and Tobago (in May) and Guyana (from November-April) (Ffrench 1991, Sullivan *et al.,* 2009).

within the period of low rainfall when the birds in Central and W South America start to gather for breeding. In July, eggs and even nestlings are found throughout the S of Amazon River in Amazonas, Pará, Mato Grosso, Tocantins and Goiás states, and Peru. The peak of the breeding season in the Southern Hemisphere in South America occurs from July to September. From October to December, we observed an increase in precipitation in this region, with the appearance of breeding colonies in N South America, where the precipitation decreases. Outside Brazil, there are fewer breeding colonies in the Paraguay, Paraná, and Uruguay River basins. They begin and end later than the other regions of SA, and unlike the other reproductive regions, rainfall seems to be well distributed throughout the year as an effect of its subtropical climate.

No breeding activity was recorded between March and May in South America, coinciding with a period of high precipitation in the continent (Fig. 4A). After the breeding season, the Black Skimmer and the Large-billed Tern migrate within and throughout South America. *Rynchops n. cinerascens* migrate mostly to coastal regions and can be found on the N Atlantic coast of Brazil, on the Pacific coast of Ecuador, Panama, Colombia, Peru, and Chile, with large flocks at the mouth of the Aconcagua River (Concon) and the Elqui River (La Serena), N and W of Argentina and in large lakes such as Titicaca in Peru and Bolivia (Davenport *et al.,* 2016). *Rynchops n. intercedens* migrates to the W Atlantic coast from the central/eastern portion of the Northern Brazilian coastline (Maranhão state) easternward to Rio Grande do Norte state, and from Bahia (Brazil) to Argentina, and also to lakes and river courses in Brazil, as well in the Mar Chiquita lagoon, Mar del Plata, which is probably the main nonbreeding concentration of *R. n. intercedens,* with around 12,000 individuals counted from late February to May (Favero *et al.,* 2001; Mariano-Jelicich *et al.,* 2003). On the other hand, *Phaetusa simplex* spp. seem to prefer the northernmost regions of South America, such as northern Colombia, Venezuela, Suriname, Guyana, French Guiana, Trinidad, Peru, and Tobago, and, in Brazil, in Pará, Maranhão, Piauí and Ceará, and its presence is common on the coastal regions of these locations. Out of the breeding season, *Phaetusa simplex* is also found in other large South American rivers, such as the Paraná, Uruguay, and São Francisco. Despite the majority of the Cuiabá River's *Phaetusa simplex* population arrival at the onset of each dry season, small numbers were also found during the flood season using the floodplain of the Cuiabá River at the SESC´s Pantanal private reserve (Antas *et al.,* 2016).

DISCUSSION

For many waterbird species, including the Black Skimmer and the Large-billed Tern, extrinsic barriers to dispersal seem to be virtually nonexistent in South America. In the case of the Black Skimmer, for instance, not even the high Andes is a hindrance to migration (Morris-Pacock *et al.,* 2010; Davenport *et al.,* 2016), and, yet, the occurrence and intratropical movements of currently accepted subspecies seem to be bounded geographically and, at least, partially affected by precipitation regimes. *Phaetusa simplex* spp., *R. niger intercedens,* and *R. niger cinerascens* complete the entire migratory cycle in South America. These populations breed during the dry season because low water levels resulting from decreased precipitation increase feeding opportunities for the young (Prance & Goulding, 1981) and expose sandbanks and sandy beaches as suitable nesting sites. Low water levels also influence habitat selection in these species because their feeding habits, resource availability, and specific foraging tactics benefit from calm flat water. Due to the discontinuous distribution in space and time of these resources and conditions, migrant species are usually concentrated in specific areas, which are of fundamental importance for their conservation (Burger & Gochfeld, 1994, 1996; Zusi, 1996; Antas *et al.,* 2016).

At the end of the breeding season – coinciding with the onset of the rainy season and the flooding of the rivers – these birds leave their breeding grounds due to unfavorable conditions, and the fishes disperse into the flooded floodplains to feed on the vegetation and forest-derived resources, thereby reducing considerably the chance for birds to obtain food resources in these areas.

Additionally, river beaches are covered by water, and these species have fewer or virtually no available resting places. Unlike variations in freshwater conditions, coastal regions always provide space, at least for resting. In the coastal regions of South America, *R. niger* can access the high productivity of near-shore marine fishing along both Pacific and Atlantic coasts (Burger & Gochfeld, 1994, 1996; Zusi, 1996; Elphick, 2007; Antas *et al.,* 2016). Pacific coastal environments have the Humboldt current that springs up near Antarctica, which is the coldest current in the world. This current runs along the coasts of Chile and Peru, and represents a rich plankton-rich resurgence zone, attracting many fish and providing a food-rich environment for *Rynchops niger cinerascens* (Bisbal, 1995; Taylor *et al.,* 2011).

Rynchops niger intercedens occurs in the coastal regions of the Eastern South Atlantic. This coastline is adjacent to one of the most productive marine environments on Earth, driven by highly productive waters, such as the mouths of the Amazon and La Plata rivers (Miloslavich *et al.,* 2011), the Atlantic Ocean counterpart of the Humbold current – the also cold-water Malvinas or Falkland current – and by resurgence zones in coastal regions such as Cabo Frio (RJ, Brazil). The cold-water mass that appears near this resurgence has high concentrations of nutrients, drawing large clusters of small pelagic fish, such as sardines (Bisbal, 1995; Miloslavich *et al.,* 2011).

According to Barbieri (2007), *R. niger intercedens* was a constant bird throughout the year in the estuary of

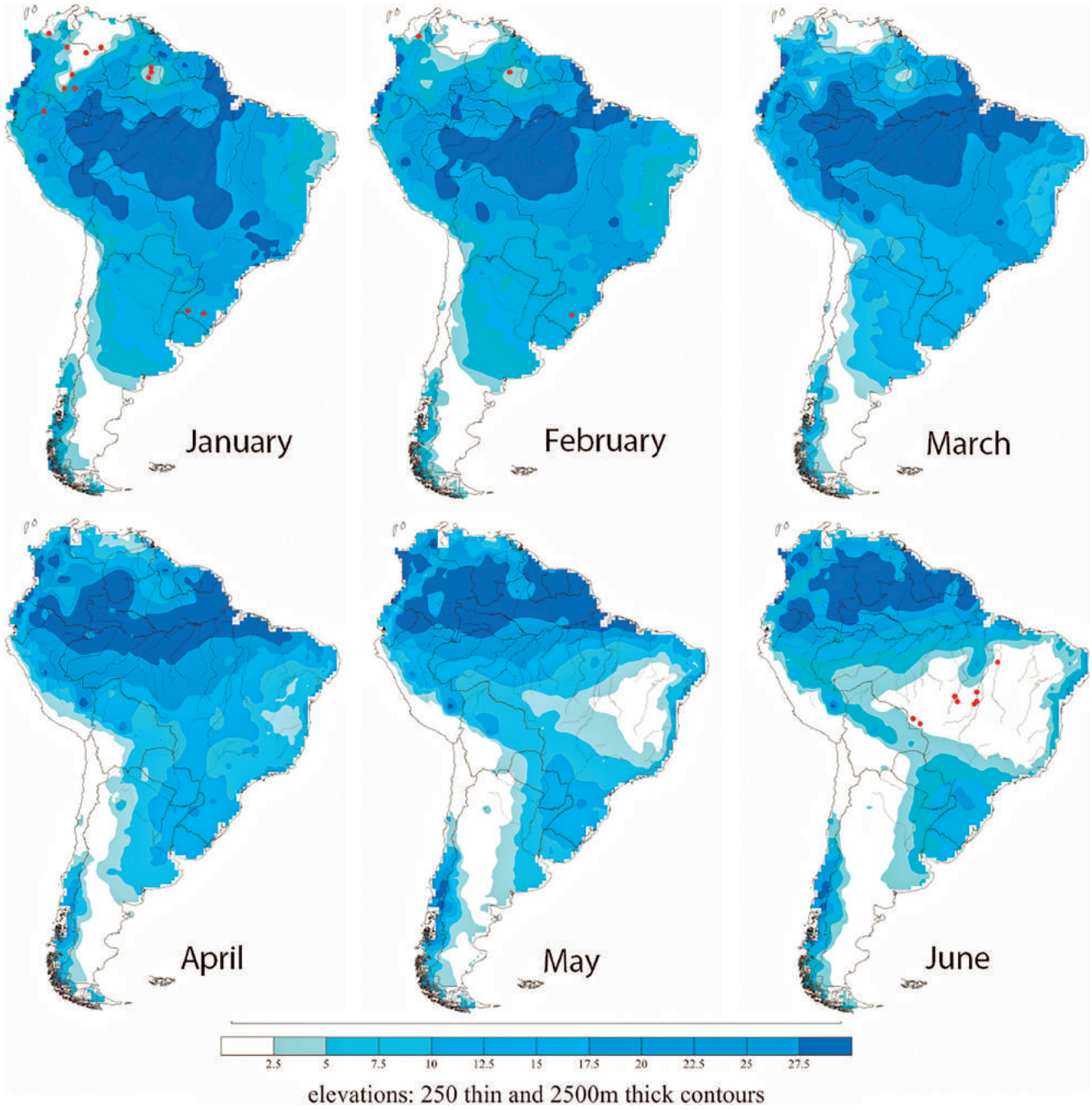

Figure 4A. Breeding sites of Black Skimmer *(R. niger)* and Large-billed Tern *(P. simplex)* in South America correlated to rainfall throughout the year (January-June). The color scale corresponds to the precipitation volume. Precipitation layers following Matsuura (2017).

Cananéia, Iguape, and Ilha Comprida (São Paulo state, Brazil). However, it showed marked fluctuations throughout the year, being more abundant in the summer, when the production of *Anchoviella lepidentostole* increases. Except for the coastal areas of northern South America and Rio Grande do Sul, the southernmost Brazilian state coastline, the Large-billed Tern seems to avoid the other coastal areas of most of the continent, giving preference to inland lakes and rivers, and, unlike the Black Skimmer, is frequently seen perched on branches in the middle of rivers, which gives an additional resting area. Electric cables and wires crossing rivers and flooded areas are also used as perches.

Antas *et al.* (2016) banded over 1,800 individuals of *R. n. intercedens* and 1,362 of *P. simplex* in the Pantanal (zone 3 in Fig. 3), several of which provided important data about migration. In the case of *R. n. intercedens,* 156 of the banded individuals who were still young returned to the banding site as adults. Data provided by Antas *et al.* (2016) indicate that at least some of the birds that nest in the Pantanal tend to migrate to the South, and some banded birds have been recovered from Torres Beach (Rio Grande do Sul state, RS), Tramandaí beach (RS), Lagoa do Peixe (RS) and, in Argentina, in the Atlantic coast of the Province of Buenos Aires at San Lorenzo del Tuyú and Mar Chiquita, Mar del Plata. The latter case was that of a banded individual captured after seven years, approximately 2,300 km from the area where it was born (Antas *et al.,* 2016).

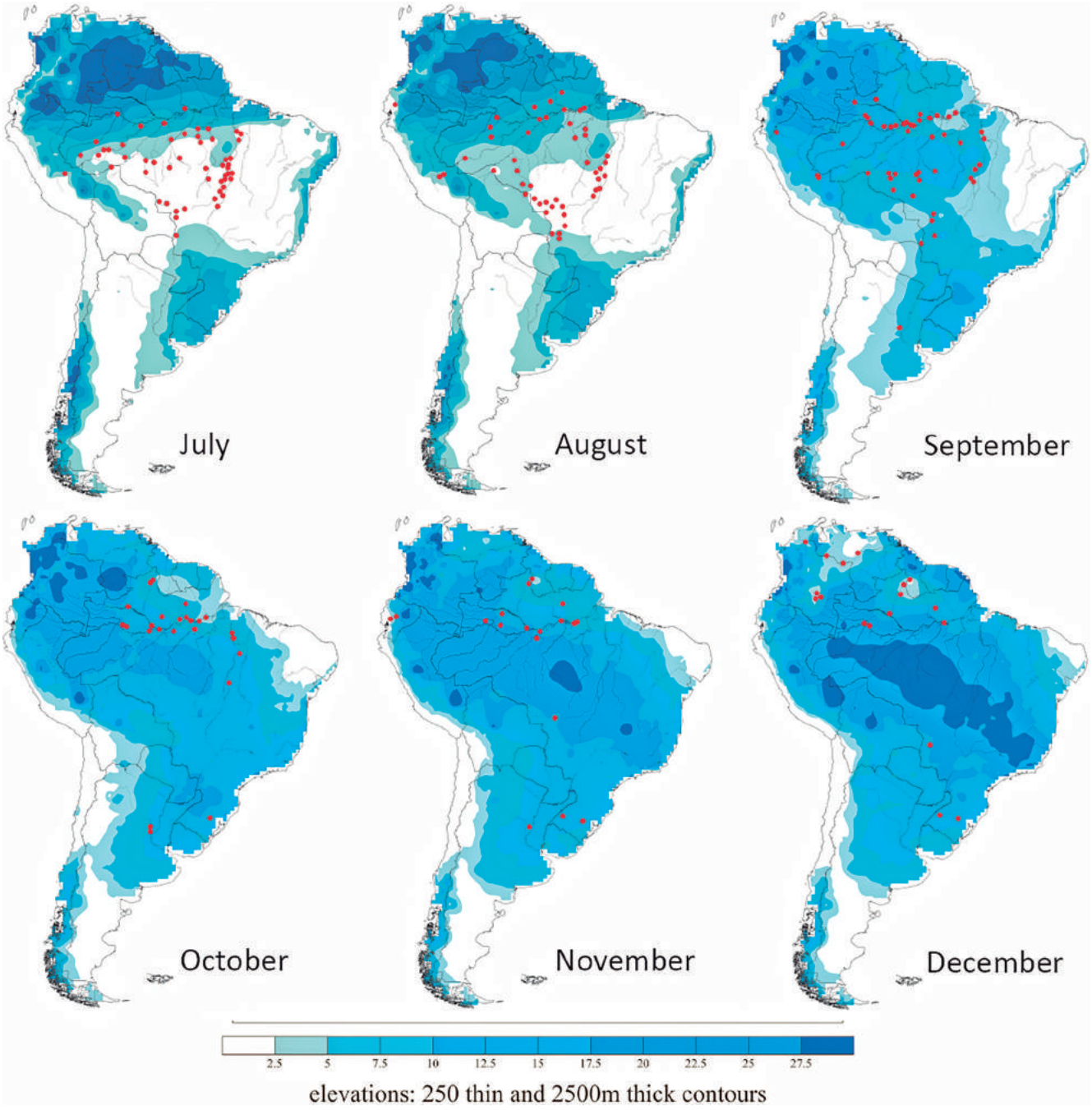

Figure 4B. Breeding sites of Black Skimmer *(R. niger)* and Large-billed Tern *(P. simplex)* in South America correlated to rainfall throughout the year (July-December). The color scale corresponds to the precipitation volume. Precipitation layers following Matsuura (2017).

Although these recaptures of banded individuals represent important data that reveal a "starting and a finishing migration point", so far, migration routes of these individuals remain unknown but can be speculated based on river dynamics, lakes, and resource availability. It is possible, for instance, that *R. n. intercedens* departs from the Cuiabá River toward the coastal region of Rio Grande do Sul, Uruguay, and Argentina through the mid and lower Paraguay River. An indication of this route would be the adequate conditions of the dynamics of these rivers and the availability of food resources, as well as the geographic distribution records of *R. n. intercedens* along with this in the Ibicuí and Jacuí rivers, and along the coast of Rio Grande do Sul. Another indication of this route as being the most likely is that there are no records of *R. niger* in the plateau of Rio Grande do Sul, Brazil (Belton, 1994; Antas *et al.,* 2016). It is likely that nesting individuals in zone 4 (RS) will move towards the Mar Chiquita (Mar del Plata, Argentina), the Patos and Peixe Lagoon, and/or the coast of Rio Grande do Sul. There are records of waterfowl using this route, such as the Rosy-billed Pochard (*Netta peposaca*) and the Fulvous Whistling-Duck (*Dendrocygna bicolor*) (Antas, 1994; Nascimento *et al.,* 2000).

Despite these emerging general patterns of intratropical migration by Black Skimmers, recent banding (RDS, 2015; Antas *et al.,* 2016) and satellite telemetry (Davenport *et al.,* 2016) studies have shown that these birds have a great dispersion capacity leading to records outside their expected area of occurrence based on plumage features. Approximately 800 *R. n. cinerascens* were banded on a beach connecting the Solimões and Japurá rivers, in Uarini, Amazonas State, Brazil. A few hundred young birds were banded and returned to the banding site as adults suggesting a certain level of philopatry, but one individual was recovered dead almost 4,000 kilometers away in southern Uruguay off the coast of La Barra (RDS, 2015). Similarly, Davenport *et al.* (2012, 2016) shed light on the hitherto unknown route of Black Skimmers by using satellite telemetry on eight individuals of a breeding colony in the Peruvian Amazon (Manu river plains). Of these individuals, three made at least the partial migration route – before the equipment stopped working – and one made the complete migration back to the marking site crossing the Andes to the Peruvian coast. Additionally, one of these individuals of *R. n. cinerascens* moved southeastward from the Manu River to the Northern Paraguayan Chaco, where the equipment stopped working. Although considered an uncommon encounter, it is possible to find individuals of the *R. n. cinerascens* where we would expect to find *R. n. intercedens,* and vice versa.

However, these extralimital records are not frequent and in most of cases correspond to young individuals or birds in nonreproductive plumage. For instance, two adults collected in 1903, in Argentina, one from San Vicente (AMNH 747804) and the other from Rio Amores (AMNH 747805), both within a short distance of the Paraná River, show a typical plumage of *R. n. cinerascens,* in a location where *R. n. intercedens* is expected. In 1945, a female belonging to *R. n. intercedens* was collected in the Zuata Reservoir in Aragua state, Venezuela (COP 30948). A young *R. n. cinerascens* that was banded in the Amazonia was found dead in Uruguay (RDS, 2015). A *Rynchops n. cinerascens* was found in the Pantanal in September 2013 (Antas *et al.,* 2016). Other records of the two subspecies occurring simultaneously were also made in Brazil: in Precabura lagoon in Ceará, in Macau in Rio Grande do Norte, and along the coast of Maranhão, where flocks with more than 300 individuals – mostly young with resting plumage – were recorded. In these regions despite the presence of some individuals belonging to *R. n. cinerascens,* the majority belonged to *R. n. intercedens* (Wikiaves data and personal observations). Of these records, only the *R. n. cinerascens* recorded in the Pantanal was in a reproductive zone.

Before Davenport *et al.* (2016), some authors such as Hughes (1970) believed it was improbable that Black Skimmers would migrate to the Peruvian coast, given the high geographical barrier imposed by the Andes and the desert habitat of much of the route before arriving on the Pacific coast. Thus, these authors assumed that *R. niger* arriving on the coast of Peru was possibly from North America. However, Davenport *et al.* (2016) showed that transandean migration of Amazonian birds indeed occurs and that migrants arriving on the coast of Peru and Chile are *R. n. cinerascens* and not *R. n. niger,* suggesting that high elevations and low temperatures do not limit movements of Black Skimmers. Additionally, migrations across elevational barriers are already known for other species such as Arctic Tern (*Sterna paradisea*) crossing the Andes (Duffy *et al.,* 2013), the Brent Geese (*Branta bernicla hrota*) overflying central highlands in Greenland (Gudmundsson *et al.,* 1995), the Bar-headed Geese (*Anser indicus*) overflying the Himalayas in Asia (Hawkes *et al.,* 2011, 2013), and several coastal birds that regularly appear in the Andes in habitats over 3,000 meters.

Nesting birds linked to the water cycles of the great rivers of South America show a complicated temporal mosaic of habitat and feeding conditions and must have movement patterns that optimize the location and regions that offer regional opportunities. Based on the data collected by this and other projects, it was possible to identify some of the main breeding areas (Myers *et al.,* 1987; Antas, 1994; Webster & Marra, 2005; Davenport *et al.,* 2016). However, despite efforts, the migratory routes, as well as corridors used by these birds, must be studied in further detail.

It could be speculated that the individuals of the Large-billed Terns that breed in the Pantanal (zone 3) and the south (zone 4) tend to migrate to the southernmost regions of the continent, given that other waterfowl undergo migrations in the Paraná watershed and southern Brazil to Paraguay, Argentina, and Uruguay (Antas, 1994). This speculation is plausible because, according to Antas *et al.* (2016), "to be in the Pantanal mid-year favors the use of the optimal period of resource supply while going to the Paraná River valley and its watershed at the end of the year, allows obtaining food resources more easily". Considering only the shortest distance as

the main migratory driver, perhaps individuals breeding in the Amazon (zone 1) would likely migrate to the northern coastal lowlands and wetlands of the continent (Colombia, Venezuela, the Guyanas coast, or the Brazilian northern coast), or major northern lakes (Tota, Fúquene, and Valencia lakes in Colombia and Venezuela). Those that breed in the Tocantins-Araguaia watershed (zone 2) likewise would migrate to the northern coastal regions of Guyana, Suriname, French Guyana, and Brazil.

CONCLUSIONS

The breeding and intratropical movements of the *P. simplex* and the South American *R. niger* taxa are affected by precipitation regimes and resource availability. The Nearctic region has marked seasonal changes and the migratory patterns of the Nearctic birds can be traced more easily, as the flocks "need" to move simultaneously to obtain the necessary resources for survival, which become scarce or nonexistent during winter. On the other hand, in portions of the Neotropics, seasons do not differ abruptly and resources are almost always available. Additionally, the South American precipitation system is characterized by a well-defined rainy season (in the summer) and a dry season (in the winter) but can vary – in frequency and intensity – from year to year. Thus, annual variations in rainfall and relatively abundant resource availability also interfere in attempts to infer migration patterns of Neotropical birds. Determining a migration pattern for these taxa proved to be a difficult task, as they disperse not in large flocks after the reproductive period. Apparently, each individual or small group may decide to take alternative routes to reach the same destination, choosing areas that provide them with resources, which can be found at various points across South America. However, although migration patterns of these South American birds have not yet been well determined, identifying the main breeding and wintering areas used by these birds represents a critical step toward understanding intratropical migration of SA waterbirds. Finally, the integration of complementary techniques, such as museum-based distribution analyses and citizen science, proved to be efficient for this task and can contribute significantly to successful management plans and conservation of these birds.

AUTHORS' CONTRIBUTIONS: ACG: Conceptualization, Methodology, Investigation, Visualization, Formal Analysis, Writing – original draft; LFS: Funding acquisition, Resources; ACG, LFS, PTZA: Data Curation; ACG, LFS, GAB: Writing – review & editing; ACG, GAB, PTZA, KLS: Validation; LFS, GAB: Supervision. All authors approved the final version of the paper.

CONFLICTS OF INTEREST: Authors declare there are no conflicts of interest.

FUNDING INFORMATION: This work received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (Project #2017/23548-2), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Frank Chapman Memorial Fund of the AMNH, and Coordenação de Aperfeiçoamento do Pessoal de Nível Superior (CAPES) for providing grants to LFS (CNPq #457974-2014-1, #302291/2015-6 and #308337/2019-0) and ACG (on the Doctoral Sandwich Programme, PDSE).

ACKNOWLEDGMENTS: The authors are grateful to Sisbio/ICMBio/MMA and to the ethical committee of animal studies from Universidade de São Paulo for providing authorizations. We thank the following institutions, curators, and staff for kindly receiving us and providing access to the specimens under their care: MZUSP, BNHM, COP, EBRG, IAVH, ICN, MNRJ, MOFURG, MPEG, AMNH, MCZ, NRM, and ZSM. We are particularly grateful to Scott V. Edwards, Jeremiah Trimble (MCZ, Harvard University), Thomas Trombone, Paul Sweet, and Joel Cracraft (AMNH). To the contributors to platforms such wikiaves and e-bird. The RPPN SESC Pantanal. Finally, Patrícia de Jesus Faria, Tânia Raso, Luciana Surita, Renata Boccorni, Julian Quitiaquez, Edson Endrigo, Marcelo Pádua, Bruno Ehlers, Wilson Lemos de Morais Neto, Vinícius de Souza, Patricia Mancini, Flavia Termignoni, Dione Seripierri and staff of Fazenda Fartura (PA) and Fazenda Descalvados (MT), and the students from the Bird section of MZUSP for helping us in the collection of specimens.

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SUPPLEMENTARY MATERIAL

https://zenodo.org/record/8309254

Annex 1: Skins of *Rynchops niger* analyzed in this study.

Annex 2: Skins of *Phaetusa simplex* analyzed in this study.

Published with the financial support of the "Programa de Apoio às Publicações Científicas da Universidade de São Paulo"