

## RESEARCH ARTICLE

# Migration in Rufous-Collared Sparrows (*Zonotrichia capensis*) from the Southernmost Tip of America

Simeon Lisovski<sup>1</sup>  | John Wingfield<sup>2</sup> | Marilyn Ramenofsky<sup>2</sup> | Omar Barroso<sup>3,4</sup> | Juan Rivero de Aguilar<sup>3,4,5</sup> | Carlos E. Valeris-Chacín<sup>3,4</sup> | Rocío Jara<sup>6</sup> | Francisco Aguirre<sup>7</sup> | Claudio S. Quilodrán<sup>3,8</sup> | Ricardo Rozzi<sup>3,4,9</sup> | Erik Sandvig<sup>5,10,11</sup> | Rodrigo A. Vásquez<sup>3,5</sup>

<sup>1</sup>Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Polar Terrestrial Environmental Systems, Potsdam, Germany | <sup>2</sup>University of California, Department of Neurobiology, Physiology and Behavior, Davis, California, USA | <sup>3</sup>Cape Horn International Center for Global Change Studies and Biocultural Conservation (CHIC), Puerto Williams, Chile | <sup>4</sup>Universidad de Magallanes, Centro Universitario Cabo de Hornos. O'Higgins 310, Puerto Williams, Chile | <sup>5</sup>Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile | <sup>6</sup>Co-Laboratorio ECOS (Ecosistema-Complejidad-Sociedad), Centro UC de Desarrollo Local (CEDEL) & Centro de Estudios Interculturales e Indígenas (CIIR), campus Villarrica, Pontificia Universidad Católica de Chile, Villarrica, Chile | <sup>7</sup>Centro de Investigación Gaia Antártica (CIGA), Universidad de Magallanes, Punta Arenas, Chile | <sup>8</sup>Department of Genetics and Evolution, University of Geneva, Geneva, Switzerland | <sup>9</sup>Sub-Antarctic Biocultural Conservation Program, Department of Philosophy and Religion, and Department of Biological Sciences, University of North Texas, Denton, Texas, USA | <sup>10</sup>Centro Bahía Lomas, Facultad de Ciencias, Universidad Santo Tomás, Chile | <sup>11</sup>Red de Observadores de Aves y Vida Silvestre de Chile (ROC), Chile

**Correspondence:** Simeon Lisovski ([simeon.lisovski@awi.de](mailto:simeon.lisovski@awi.de))

**Received:** 9 July 2024 | **Revised:** 6 February 2025 | **Accepted:** 12 February 2025

**Funding:** This work was supported by ANID Convocatoria Nacional Subvención a Instalación en la Academia Convocatoria Año 2020, N°PAI77200078 CONICYT, ANID/BASAL-CHIC- FB210018.

**Keywords:** austral migration | differential migration | geolocators | *Zonotrichia*

## ABSTRACT

Little is known about the routes, timing and potential drivers of migration among austral migrants of South America. To contribute to a better understanding, we studied the migration of the southern subspecies of Rufous-collared Sparrow (*Zonotrichia capensis australis*) from the southernmost tip of South America. Based on 11 tracks, we found that departure from the breeding grounds in fall (post-breeding migration) occurred within a wide temporal window, beginning on March 22 and finishing on May 17. Wintering grounds were identified between 51.2°S and 31.9°S, within the Patagonian steppe ecoregion. Migration distance ranged from 450 to 2500 km, with the longest distance registered for two females who were the first to depart for the outbound route and the latest to arrive at the breeding grounds upon their return, offering an indication of a differential migration pattern.

## 1 | Introduction

The number of terrestrial birds migrating towards their breeding sites in the northern hemisphere is greater than their southern hemisphere counterparts by a large margin (Chesser 1994). The smaller land masses in the south may result in fewer migratory species. Seasonality, the ultimate driver of migration across latitude, is in addition less pronounced and less predictable on the southern continents compared to the north

(Lisovski et al. 2017), suggesting that migration may partly be motivated by different environmental factors in different hemispheres (Jahn et al. 2010). However, with > 230 species that migrate entirely within South America (Stotz et al. 1996), the continent hosts one of the most diverse migration systems on Earth (Chesser 1994; Jahn et al. 2004, 2020). Studies have shown that migration in South America is surprisingly complex and is not simply a mirror image of the intensively studied and well-understood Nearctic–Neotropical system of North

America (Jahn et al. 2004, 2020). The types of migration systems in South America include migrations between temperate breeding grounds and the tropics, migration wholly within tropical latitudes or temperate latitudes, elevational migration, and longitudinal migration (Chesser 1994; Areta and Bodrati 2008; Cueto et al. 2009; Faaborg et al. 2010; Jiménez et al. 2016; Jahn et al. 2020).

The White-crowned Sparrow (*Zonotrichia leucophrys*), distributed across North America, exhibits some of these migration types (Chilton et al. 1995; Morton 2002). Different sub-species express different migration strategies, ranging from sedentary (*Z. l. nuttalli*) to short latitudinal and altitudinal (*Z. l. pugetensis*), intermediate and altitudinal (*Z. l. oriantha*), and long-distance migration (*Z. l. gambelii*) (Lisovski et al. 2019). The Rufous-collared Sparrow (*Zonotrichia capensis*), from Central and South America, a congener species of the White-crowned Sparrow, is one of the most polytypic avian species, with more than 20 described subspecies (Chapman 1940; Zink 1982) that also show variation in migration strategies (Chapman 1940), but is far less studied and understood. The latter species is one of the most wide-ranging New World birds, distributed from Chiapas, Mexico (10°N) to the southern tip of South America (56°S). It breeds in virtually all open habitats, from sea level to more than 4000 m.a.s.l., absent only from continuous humid forests, including much of the Amazonian basin (Chapman 1940). Most populations, including those inhabiting lowland tropical deserts and Mediterranean biomes, appear to be sedentary (Moore et al. 2005; Chapman 1940; Miller 1959; Class 2009; Class et al. 2011; González-Gómez et al. 2013, 2018; Pyle et al. 2015; Cueva 2018; Poblete et al. 2018, 2023; Valeris-Chacin 2023). Other populations from central South America, such as the altiplano and the Andes populations in southern Bolivia and northern Argentina and Chile, undergo altitudinal or no migration at all (Poblete et al. 2018, 2023), and the southern subspecies (i.e., *Z. c. australis*) is a long-distance latitudinal migrant (Chapman 1940). However, very little is known about the Rufous-collared Sparrow's migration phenology, destinations, routes and population variation.

During the breeding season in December 2017, we equipped Rufous-collared Sparrows (*Z. c. australis*) on one of the southernmost islands of South America, Navarino Island, Cape Horn, Chile (55°S), with light-level geolocators to track their seasonal movements. Based on the tracks, we here aim to provide information regarding migration schedules, including departure dates in autumn and arrival dates in spring. Moreover, we relate environmental conditions (temperature and precipitation) to migration phenology to understand the environmental context within the migration of this Rufous-collared Sparrow's austral subspecies.

## 2 | Methods

### 2.1 | Fieldwork

We conducted fieldwork on Navarino Island, Chile (63.30°W, 54.93°S) within the Cape Horn Biosphere Reserve, which encompasses a mosaic of grasslands, Magellanic forest, peat bogs, lakes, beaches, and alpine vegetation. The field sites included the

northern limits of the island from Eugenia Bay (east) to Puerto Navarino (west) (0–50 m.a.s.l.) along the main road (75 km), and Cerro Bandera hill (500–600 m a.s.l.) (Figure 1). During the breeding season (November to December) of 2017–2018, we captured with mist nets 60 adult Rufous-collared Sparrows (46 males and 14 females). Each bird was identified individually with an aluminium band and a colour plastic band to differentiate the sex (blue = male, red = female). We assigned the sex for males by the presence of a prominent cloacal protuberance (width and length > 5 mm) and females by the presence of a brood patch (see González-Gómez et al. 2013). We deployed a leg-loop harness system to attach the loggers (manufactured by the Swiss Ornithological Institute, Version GDL3). After processing the birds, we released them in the same location where they were captured and observed each bird during its release to verify that the device did not interfere with its ability to fly. The weight of the loggers with the harness was between 0.6 and 0.8 g, corresponding to 2%–4% of the bird's body mass. Hence, we expected very small or no effects on the birds' survival, reproduction, and behaviour (see Brlík et al. 2020). During the two subsequent austral spring–summer seasons (2018/2019 and 2019/2020) the area was searched repeatedly for individuals carrying a geocator to capture and retrieve the device.

Permits to capture, handle, and attach geolocators to birds for research were approved by Servicio Agrícola y Ganadero (SAG) (Resolución Exenta Nos. 8084 No: 8084/2017, 3813/2018, 5496/2019 and 5224/2020). All methods were performed in accordance with the guidelines from the Biosecurity Manual of CONICYT (version 2008), the Chilean law No. 20380 about animal protection, the use of wild birds in research (see Fair et al. 2010), and following the SAG banding ethical protocol.

### 2.2 | Geolocation

After logger retrieval, we downloaded and analysed the data using the R packages *TwGeos* (Lisovski et al. 2015) and *SGAT* (Wotherspoon et al. 2013) in R (R Development Core Team 2016). First, the twilight events were defined using a light intensity threshold of 1 (arbitrary units). Strong outliers were removed and flagged in the available data files. For each individual, twilight events from the beginning and the end of the dataset that were definitely recorded at the breeding site were used for on-bird calibration to derive the reference zenith angle and the parameters for the twilight error gamma distribution (for more information, see: Lisovski et al. 2020). Next, we estimated the likelihood that each defined sunrise and sunset time was recorded on the breeding site by using the gamma density distribution function from the individual calibration. During the subsequent location estimation process using MCMC simulations from the R package *SGAT*, the twilight times before and after the first and last twilight that were not recorded at the breeding site (with a probability of  $p > 0.99$ ) were fixed to the breeding location. The primary purpose of this step was to avoid movement estimations due to differences in shading over time. This was only implemented after realising the large errors in detecting twilight events, resulting in likely false northward movements during the fall equinox when the birds were most likely resident on their breeding sites. We used a spatial mask that prevented location estimates on the ocean and a gamma movement



**FIGURE 1** | Southern tip of South America, with Island Navarino (coloured in yellow) where fieldwork was conducted in the northern limits of the Island (map based on the Natural Earth dataset).

**TABLE 1** | Migration summary of the analysed Rufous-collared Sparrow breeding on Navarino Island (Chile). Departure and arrival dates are estimations that should not be treated as exact dates ( $\pm 5$  days). The distance refers to the estimated median migration distance between the breeding and the major non-breeding site. Photoperiods are expressed in decimal hours, and temperature in degrees Celsius.

ID	Sex	Departure (yyyy-mm-dd)	Arrival (yyyy-mm-dd)	Median Distance (km)	Total days outside breeding ground	Time outside breeding ground (%)
LL	F	2018-03-22	2018-10-05	1689	197	54
LB	F	2018-03-25	2018-09-18	2568	177	48
FT	M	2018-04-01	2018-08-20	2058	141	39
LO	M	2018-04-09	2018-09-07	1912	151	41
LC	M	2018-04-17	2018-08-12	457	117	32
GL	M	2018-04-18	2018-09-05	1360	140	38
GY	M	2018-04-19	Unknown	1603	Unknown	Unknown
HI	M	2018-04-24	2018-08-28	1392	126	35
LP	M	2018-04-29	2018-08-23	2378	116	32
GB	M	2018-05-07	2018-08-12	463	97	27
GR	M	2018-05-09	2018-08-28	1900	111	30
GT	M	2018-05-17	2018-08-03	992	78	21

model with scale=1 and rate=0.5. The proposals (starting points for the MCMC simulations) were first tuned using relaxed assumptions and 2000 iterations, followed by another tuning of the restricted mode and 900 iterations. The final run consisted of 2000 iterations. To estimate departure and arrival dates, we used the first and last twilight time recorded on or close to the breeding site ( $p < 0.99$ ). Investigations of the track estimates led to the assumption that all birds migrated relatively quickly to

a final destination and remained within an area for which the accuracy of the estimates was too low to determine smaller-scale movements. Based on this assumption, we used the final 2000 MCMC chains for the entire period of track estimates not fixed to the breeding site to calculate the estimates' 20, 50, and 80 percentiles (e.g., the final migration destination). Raw data, annotated twilights, estimated locations, and the custom R code are available at [www.movebank.org](http://www.movebank.org) (Movebank ID: 1069351291).

## 2.3 | Environmental Variables

We downloaded ECWMF ERA5 reanalysis near surface temperature (2m) and precipitation/rainfall data (European Centre for Midrange Weather Forecast, <https://www.ecmwf.int/>) for the larger region around Navarino Island ( $\text{lon}_{\text{max}} = -68.65$ ,  $\text{lon}_{\text{min}} = -66.85$ ,  $\text{lat}_{\text{min}} = -54.08$ ,  $\text{lat}_{\text{max}} = -55.58$ ) and for February to June (post-breeding departure period) and July to November (pre-breeding arrival period). Both temperature and rainfall data were downloaded for eight time stamps per day (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00 and 21:00) and summarised to derive mean daily temperature and the sum of daily rainfall. Daily daylength (photoperiod) was calculated using the R Package GeoLight (Lisovski et al. 2020).

## 3 | Results

### 3.1 | Fieldwork

Sixteen of the 60 birds (13 males and 3 females) were recaptured during the austral summer seasons 2018/19 ( $N=14$ ) and 2019/20 ( $N=2$ ). There were no differences in recapture rates between males and females ( $\chi^2 = 0.257$ ,  $df=1$ ,  $p\text{-value}=0.612$ ). One male and one female were observed with geolocators, and we tried to recapture them with no success. We used playbacks of pre-recorded Rufous-collared Sparrow's songs and one Rufous-collared Sparrow decoy to attract birds to the mist nets. Although both males and females actively responded to the playback and decoy, it is possible that females remained at a greater distance and for a shorter duration, leading to less frequent captures. Both males and females showed clear signs of breeding activity (territorial behaviour and brood patch). All individuals

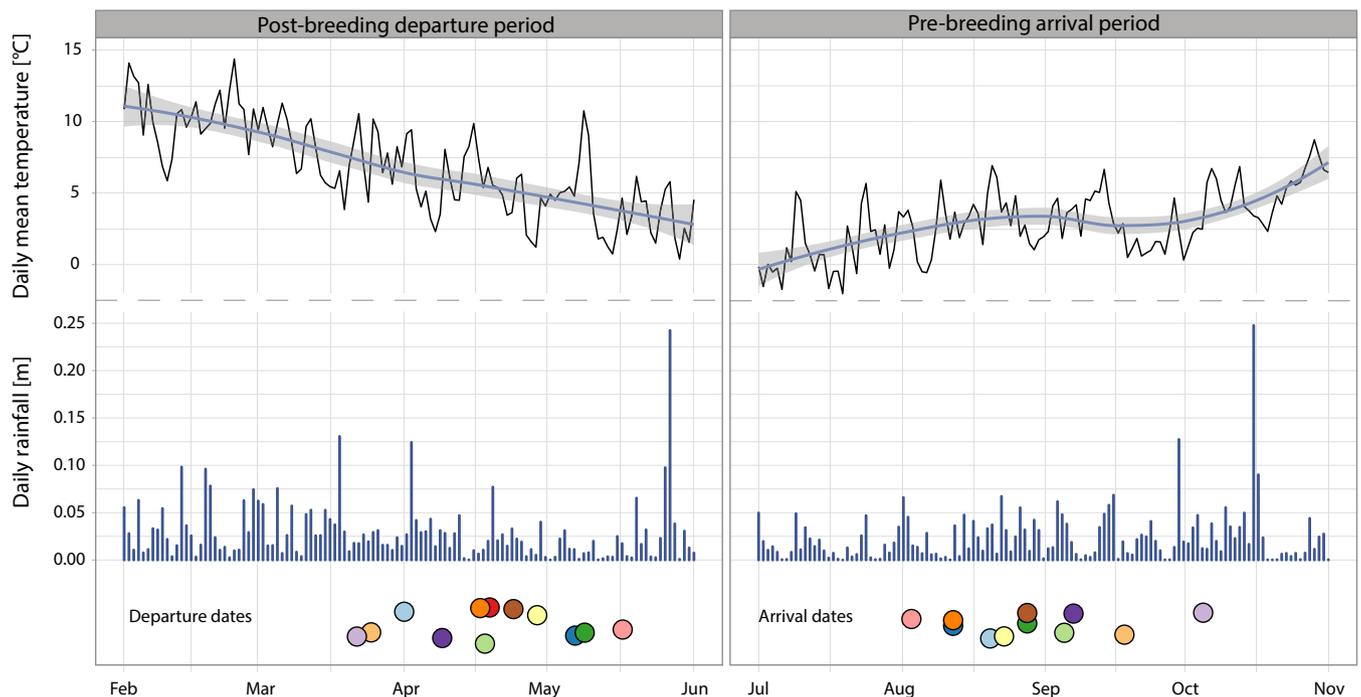
where recaptured in the same area where initially captured. Data from 5 of the 16 samples could not be downloaded due to logger failure. One individual (GX) lost its logger, recordings from two birds were incomplete (LA and GY), and two sensors (GM, GC) were either faulty or completely obscured by feathers. Thus, we based our analyses on 11 (2 females and 9 males) complete and one partial track (Table 1).

### 3.2 | Phenology

Birds left the breeding area between 22 March and 17 May (57 days; mean: 17 April 2018) (Figure 2a, Table 1). Return dates to the breeding ground ranged from 3 August to 5 October (64 days; mean: 28 August 2018). Females were the first to depart (mean females: 23 March,  $n=2$ ; mean males: 24 April,  $n=10$ ) and had the latest return (mean females: 26 September; mean males: 22 August). The time window between the last departure and the first return was 77 days.

### 3.3 | Environmental Conditions

The photoperiod during the post-breeding departure period varied from 12.0 to 8.2h (22 March to 17 May, Table 1), with a difference of 3.4h. Maximum temperatures within the departure period (Figure 2) varied from 14.9°C to 4°C (mean: 9.3°C, SD: 3.17) and minimum temperatures from 9.4°C and to -2.3°C (Mean: 2.4°C, SD: 2.76). The photoperiod during pre-breeding arrival ranged between 8.6 h (first arrival in August) and 13.1 h light on the last arrival date (registered on October 05th), with a difference of 4.5h. Maximum temperatures ranged from 1.4°C to 12°C (mean: 7°C, SD: 2.66) and minimum temperatures from



**FIGURE 2** | Daily mean temperature (°C) with a smooth line and the amount of daily rainfall (m) within the larger region of the breeding area of Isla Navarino (Chile), for the post-breeding departure period (left) and the pre-breeding arrival period (right). The lower coloured points refer to individual post-breeding departure and pre-breeding arrival dates (colour scheme is shown in Figure 3b).

−4°C to 5.3°C (mean: 0°C, SD: 2.22). Both during the post-breeding departure period and the pre-breeding arrival period, rainfall patterns (Figure 2) were highly variable, with a mean daily rainfall (within the entire region) of 28 mm and 23 mm, respectively (maximum of 242 mm and 247 mm).

### 3.4 | Migration

During post-breeding migration in autumn, all birds migrated northwards to western Argentina except for one (LL) who resided in eastern Chile (Figure 2b, Table 1). Migration distance between the breeding and non-breeding grounds ranged from approximately 450 to 2500 km. Two males (GB, LC) remained in close proximity to the breeding area in southern Argentina north of Tierra del Fuego. All others migrated at least 1000 km north but settled within a large latitudinal (51.2°S–31.9°S) and along a relatively narrow longitudinal range (71.0°–66.5°W) east of the Andes and far from the coast of the Atlantic ocean. The two females (LL and LB) resided in the upper half of the northerly range (Figure 3b).

## 4 | Discussion

In this study, we investigated the migratory patterns of Rufous-collared Sparrows breeding in southern Chile. We observed broad differences in the migratory phenology and migration patterns among individuals. Our results indicate a large inter-individual range of migration distances in this species, similar to those reported for its congener, the White-crowned Sparrow in North America (Lisovski et al. 2019).

Although the breeding grounds are in the most austral latitude for this species, the lower seasonality, compared to the breeding locations for White-crowned Sparrows in the northern hemisphere (which breeds at higher latitude), may explain the high variation of post-breeding departure dates (Lisovski et al. 2019). Furthermore, the White-crested Elaenia, a sympatric long-distance migrant that also breeds at the same latitude, exhibits a similar variation in departure dates (49 days) (Jara et al. 2024). The high variation of departure dates of the Rufous-collared Sparrow and the environmental seasonality of Navarino Island suggested that photoperiod, temperature, and rainfall are not so determinant cues for migration timing, or at least not for all individuals. Nonetheless, the temporal window during which Rufous-collared Sparrows were outside Navarino island, with a photoperiod below 8 h and mean temperatures below 0°C, suggested both are limiting factors for this population. In other words, local and regional weather conditions may not provide proximate cues for departure but do provide ultimate causation for moving north in autumn and winter. What explains such variation in post-breeding departure dates (and arrival dates) remains unknown.

Migration routes were mainly parallel to the east side of the Andes Mountain range. The local variation of non-breeding ground locations among the individuals and migration distances may be attributed to the homogeneity of the Patagonian steppe Ecoregion (i.e., the Patagonian phytogeographic province) (Bisigato and Bertiller 2020) within the temperate

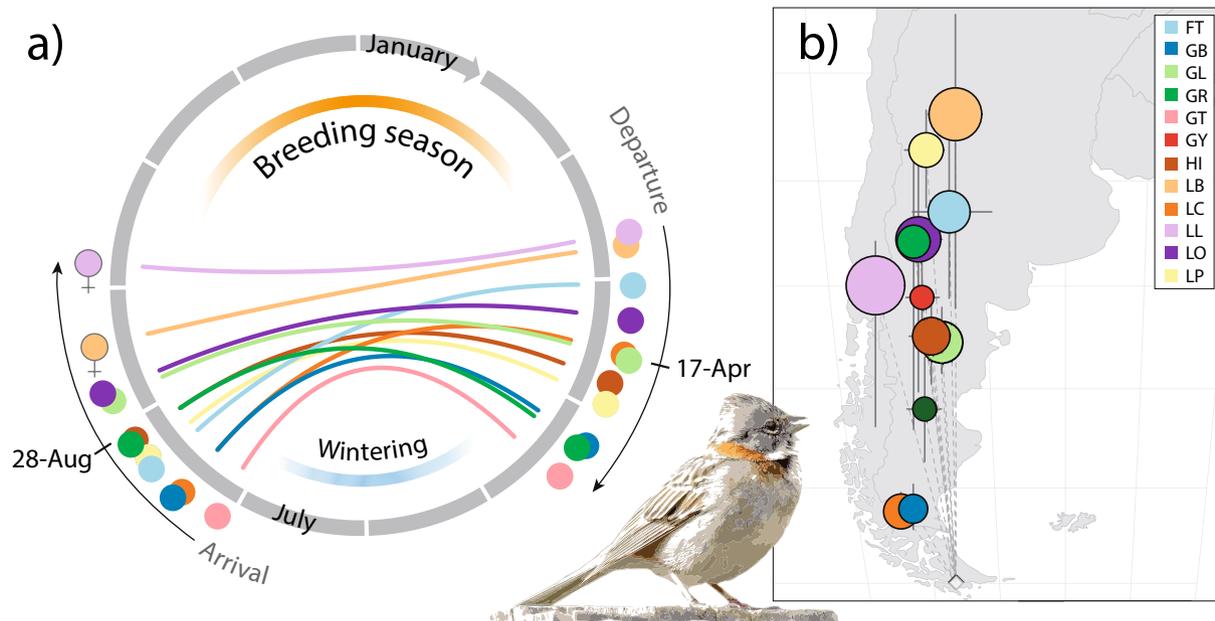
grassland, savannas, and shrublands biomes. The climate of the Patagonian steppe is semiarid cool in the Köppen climate system (Geiger, 1954, Coronato 2020). It encompasses the area where most of the individuals arrived at the end of outbound migration. Only three individuals used different habitats, one in the Andes Mountain range and two in the south, close to Tierra del Fuego Island, in the southern limit of the Patagonian steppe Ecoregion. Unfortunately, precise habitat choice cannot be inferred due to the low accuracy of the locations.

The migration patterns of the Rufous-collared Sparrow exhibit similarities and differences to those of the White-crested Elaenias breeding on Navarino Island. Both species have a large range of departure dates from the breeding ground (Jara et al. 2024). However, White-crested Elaenias leave Navarino on average almost 2 months before the sparrows (Jara et al. 2024). Finally, sparrows return to the breeding ground approximately 2 months before the White-crested Elaenias do (28 August vs. 30 October) (Jara et al. 2024).

As in most birds, moult may restrict the timing of breeding and migration; therefore, it could constrain migration phenology. In Navarino island, the Rufous-collared Sparrows pre-alternate (DPB) and pre-formative (FPF) moults take place on the breeding grounds (data from the Long Term Bird Monitoring Program at Ethnobotanical Omora Park). However, it is not possible to discount that some individuals may be in active moult during post-breeding migration, or even complete their moult in the wintering area, although in general, migratory birds mostly avoid overlapping life history stages due to very high energetic demands that would accrue (Wingfield 2007). On the contrary, White-crested Elaenias moult on the wintering grounds, which probably allows for an earlier departure from Navarino island while avoiding overlap of pre-basic moult and migration.

Interestingly, there seems to be a temporal correlation between post-breeding departure and pre-breeding arrival, with earlier departing birds arriving also later during the pre-breeding arrival period (Figure 3a). While this seems independent of the wintering sites and the distance, the two females departed first and arrived latest, thus spending considerably less time on the breeding site compared to the tracked males. In combination with the largest migration distance in one of the females (LB) and the other female also overwintering in the northern half of the detected range, we might speculate that this population of Rufous-collared Sparrows expresses some degree of differential migration between sexes, as seen in closely related species in the northern hemisphere (Ketterson and Nolan 1983). Yet, this pattern would need confirmation with a larger sample size with a higher proportion of female tracks.

In conclusion, the Rufous-collared Sparrow population from the southernmost tip of South America shows high variation in its migration phenology, suggesting an association with the high variation in individual responses to seasonal changes and environmental conditions such as photoperiod, temperature, and rainfall, possibly mediated by the low-temperature seasonality when compared with northern bird species inhabiting similar latitudes (Lisovski et al. 2017). Therefore, future studies will be needed to explore the possible differences between sexes, ages, body conditions, and reproductive status in more detail.



**FIGURE 3** | Migration phenology (a) and destinations (b) of Rufous-collared Sparrow breeding on Navarino Island (Chile). Post-breeding departure and pre-breeding arrival dates are estimated based on the likelihood that the sunrise and sunset times inferred from light-level geolocators were not recorded on and around the breeding area ( $p > 0.99$ ). The major non-breeding sites refer to the median location estimate with the 60% credibility interval of all estimates (MCMC simulation) after departure and before arrival at the breeding site. The size of the circle corresponds to the duration each individual was away from the breeding ground (78–200 days).

#### Author Contributions

**Simeon Lisovski:** conceptualization, formal analysis, funding acquisition, investigation, methodology, software, visualization, writing – original draft. **John Wingfield:** conceptualization, data curation, project administration, writing – original draft, writing – review and editing. **Marilyn Ramenofsky:** conceptualization, data curation, project administration, writing – original draft, writing – review and editing. **Omar Barroso:** data curation, formal analysis, writing – review and editing. **Juan Rivero de Aguilar:** data curation, writing – review and editing. **Carlos E. Valeris-Chacín:** data curation, writing – review and editing. **Rocío Jara:** data curation, writing – review and editing. **Francisco Aguirre:** data curation, writing – review and editing. **Claudio S. Quilodrán:** data curation, writing – review and editing. **Ricardo Rozzi:** funding acquisition, writing – review and editing. **Erik Sandvig:** data curation, writing – review and editing. **Rodrigo A. Vásquez:** conceptualization, data curation, project administration, writing – original draft, writing – review and editing.

#### Acknowledgements

J.W. acknowledges the Abate Molina Award from CONICYT, Chile. We thank the Swiss Ornithological Institute and specifically Steffen Hahn for providing the light-level geolocators as part of the project “tracking least known species.” S.L. acknowledges financial support by Geo.X, the Network for Geosciences in Berlin and Brandenburg. J.R.A., C.V., O.B., R.R., and R.A.V. acknowledge support from grant AFB-170008-CONICYT-Chile, and the Cape Horn International Center ANID/BASAL-CHIC-FB210018, and JRA to FONDECYT Postdoctorado Folio No. 3170211, and ANID Convocatoria Nacional Subvención a Instalación en la Academia Convocatoria Año 2020 Folio No. PAI77200078. We appreciate the continued collaboration and support provided by the National Forestry Corporation (CONAF) and the Servicio Agrícola Ganadero (SAG).

#### Data Availability Statement

Geolocation by light raw data, defined twilight times and estimated locations openly available at <https://www.movebank.org> (Movebank ID: 1069351291).

#### References

- Areta, J. I., and A. Bodrati. 2008. “Movimientos Estacionales y Afinidad Filogenética de la Viudita Coluda (*Muscipipra vetula*).” *Ornithologia Neotropical* 19: 201–211.
- Bisigato, A. J., and M. B. Bertiller. 2020. “Vegetation of Patagonia.” In *Lizards of Patagonia*, edited by M. Morando and L. J. Avila. Springer. <https://doi.org/10.1007/978-3-030-42752-8>.
- Brlík, V., J. Koleček, M. Burgess, et al. 2020. “Weak Effects of Geolocators on Small Birds: A Meta-Analysis Controlled for Phylogeny and Publication Bias.” *Journal of Animal Ecology* 89: 207–220. <https://doi.org/10.1111/1365-2656.12962>.
- Chapman, F. M. 1940. “The Post-Glacial History of *Zonotrichia capensis*.” *Bulletin of the American Museum of Natural History* 77: 381–438.
- Chesser, R. T. 1994. “Migration in South America: An Overview of the Austral System.” *Bird Conservation International* 4: 91–107.
- Chilton, G., M. C. Baker, C. D. Barrentine, and M. A. Cunningham. 1995. “White-Crowned Sparrow (*Zonotrichis leucophrys*).” In *In Birds of the World*, edited by A. Poole. Cornell Lab of Ornithology.
- Class, A. 2009. *Seasonality and Trade-Off in Equatorial Rufous-Collared Sparrows*. Virginia Polytechnic Institute and Virginia State University.
- Class, A., H. Wada, S. Lynn, and I. Moore. 2011. “The Timing of Life-History Stages Across Latitudes in *Zonotrichia* Sparrows.” *Condor* 113, no. 2: 438–448.
- Coronato, F. R. 2020. “Geographical Singularities of the Patagonian Climate.” In *Lizards of Patagonia*, edited by M. Morando and L. J. Avila. Springer. <https://doi.org/10.1007/978-3-030-42752-8>.

- Cueto, V. R., F. A. Milesi, M. C. Sagario, J. López de Casenave, and L. Marine. 2009. "Distribución Geográfica y Patrones de Movimiento De la Monterita Canela (*Poospiza ornata*) y el Yal Carbonero (*Phrygilus carbonarius*) en Argentina." *Ornitología Neotropical* 20: 479–490.
- Cueva, D. 2018. "Molt Strategy and Ageing of Rufous-Collared Sparrow (*Zonotrichia capensis*) in Bogotá, Colombia." *Caldasia* 40, no. 1: 18–26. <https://doi.org/10.15446/caldasia.v40n1.63337>.
- Faaborg, J., R. T. Holmes, A. D. Anders, et al. 2010. "Recent Advances in Understanding Migration Systems of New World Land Birds." *Ecological Monographs* 80: 3–48.
- Fair, J., E. Paul, and J. Jones, eds. 2010. *Guidelines to the Use of Wild Birds in Research*. Ornithological Council.
- Geiger, R. 1954. "Klassifikation der Klimate nach W. Köppen [Classification of climates after W. Köppen]." In *Landolt-Börnstein – Zahlenwerte und Funktionen aus Physik, Chemie, Astronomie, Geophysik und Technik, alte Serie. Vol. 3*, 603–607. Springer.
- González-Gómez, P., L. Merrill, V. Ellis, et al. 2013. "Breaking Down Seasonality: Androgen Modulation and Stress Response in a Highly Stable Environment." *General and Comparative Endocrinology* 191, no. 1–12: 27.
- González-Gómez, P. L., V. Echeverría, C. F. Estades, et al. 2018. "Contrasting Seasonal and Aseasonal Environments Across Stages of the Annual Cycle in the Rufous-Collared Sparrow, *Zonotrichia capensis*: Differences in Endocrine Function, Proteome and Body Condition." *Journal of Animal Ecology* 87: 1–19.
- Jahn, A. E., V. R. Cueto, C. S. Fontana, et al. 2020. "Bird Migration Within the Neotropics." *Auk* 137: 1–23.
- Jahn, A. E., D. J. Levey, J. A. Hostetler, and A. M. Mamani. 2010. "Determinants of Partial Bird Migration in the Amazon Basin." *Journal of Animal Ecology* 79: 983–992.
- Jahn, A. E., D. J. Levey, and K. G. Smith. 2004. "Reflections Across Hemispheres: A System-Wide Approach to New World Bird Migration." *Auk* 121: 1005–1013.
- Jara, R. F., J. E. Jimenez, and R. Rozzi. 2024. "White-Crested Elaenias (*Elaenia Albiceps Chilensis*) Breeding Across Patagonia Exhibit Similar Spatial and Temporal Movement Patterns Throughout the Year." In *White-Crested Elaenias (*Elaenia albiceps chilensis*) Breeding Across Patagonia Exhibit Similar Spatial and Temporal Movement Patterns Throughout the Year*, vol. 19. In Press.
- Jiménez, J. E., A. E. Jahn, R. Rozzi, and N. E. Seavy. 2016. "First Documented Migration of Individual White-Crested Elaenias (*Elaenia albiceps chilensis*) in South America." *Wilson Journal of Ornithology* 128: 419–425.
- Ketterson and Nolan. 1983. "The Evolution of Differential Migration." *Current Ornithology* 1: 357–401.
- Lisovski, S., S. Bauer, M. Briedis, et al. 2020. "Light-Level Geolocator Analyses: A User's Guide." *Journal of Animal Ecology* 89: 221–236.
- Lisovski, S., Z. Németh, J. C. Wingfield, et al. 2019. "Migration Pattern of Gambel's White-Crowned Sparrow Along the Pacific Flyway." *Journal für Ornithologie* 160: 1097–1107. <https://doi.org/10.1007/s10336-019-01685-4>.
- Lisovski, S., M. Ramenofsky, and J. C. Wingfield. 2017. "Defining the Degree of Seasonality and Its Significance for Future Research." *Integrative and Comparative Biology* 57: 934–942.
- Lisovski, S., M. D. Summer, and S. J. Wotherspoon. 2015. "TwGeos: Basic Data Processing for Light-Based Geolocation Archival Tags. Github Repository." <http://rdrr.io/github/slisovski/TwGeos/>.
- Miller, A. H. 1959. "Reproductive Cycles in an Equatorial Sparrow." *PNAS* 45, no. 7: 1095–1100.
- Moore, I. T., F. Bonier, and J. C. Wingfield. 2005. "Reproductive Asynchrony and Population Divergence Between Two Tropical Bird Populations." *Behavioral Ecology* 4: 755–762.
- Morton, M. 2002. *The Mountain White-Crowned Sparrow: Migration and Reproduction at High Altitude*. Studies in Avian Biology, 24. J. T. Rotenberry (Ed.). Cooper Ornithological Society.
- Poblete, Y., C. Contreras, C. Fernández, et al. 2023. "Geographic Variation in the Altitudinal Migration Patterns, Body Size, Oxidative Status and Exploratory Behavior in a Neotropical Bird." *Ecology and Evolution* 13: e9941. <https://doi.org/10.1002/ece3.9941>.
- Poblete, Y., V. Gutiérrez, W. Cid, S. D. Newsome, P. Sabat, and R. A. Vásquez. 2018. "Intraspecific Variation in Exploratory Behavior and Elevational Affinity in a Widely Distributed Songbird." *Oecologia* 186: 931–938. <https://doi.org/10.1007/s00442-018-4076-8>.
- Pyle, P., A. Engilis Jr., and D. A. Kelt. 2015. *Manual for Ageing and Sexing Landbirds of Bosque Fray Jorge National Park and North-Central Chile, With Notes on Occurrence and Breeding Seasonality*. Special Publication of the Occasional Papers of the Museum of Natural Science.
- R Development Core Team. 2016. "R: A Language and Environment for Statistical Computing." In R Foundation for Statistical Computing, <https://www.r-project.org/>.
- Stotz, D. F., F. W. Fitzpatrick, T. A. Parker, and K. Moskovits. 1996. *Neotropical Birds: Ecology and Conservation*. University of Chicago Press.
- Valeris-Chacín, C. E. 2023. *Reproducción y Muda de Zonotrichia capensis (Emberizidae) en un Ambiente Silvestre y Urbano de Chile Central. Importancia de la Estacionalidad Ambiental*. Facultad de Ciencias, Universidad de Chile.
- Wingfield, J. C. 2007. "Organization of Vertebrate Annual Cycles: Implications for Control Mechanisms." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 27: 425–441. <https://doi.org/10.1098/rstb.2007.2149>.
- Wotherspoon, S. J., D. A. Sumner, and S. Lisovski. 2013. "R Package SGAT: Solar/Satellite Geolocation for Animal Tracking. Github Repository." <https://github.com/SWotherspoon/SGAT>.
- Zink, R. M. 1982. "Patterns of Genic and Morphologic Variation Among Sparrows in the Genera *Zonotrichia*, *Melospiza*, *Junco* and *Passerella*." *Auk* 99: 632–649.