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Non-Breeding Distribution and Activity Patterns of Antarctic Storm-Petrels Inferred From Geolocator-Immersion Loggers and Stable Isotopes

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ABSTRACT

Outside the breeding season, small pelagic seabirds are particularly challenging to study due to their large geographic ranges and high mobility. Consequently, their non-breeding distribution and activity patterns are often poorly known. However, the non-breeding period is of critical importance, encompassing both migration and flight feather moult. We combined miniaturised geolocator-immersion loggers (GLS) with carbon and nitrogen bulk and compound-specific stable isotope analyses of rectrix feathers. Using this approach, we investigated the annual phenology, migratory routes, moult locations, non-breeding activity patterns and distribution of two Antarctic storm-petrel species: Wilson's Storm-petrel *Oceanites oceanicus* and Black-bellied Storm-petrel *Fregetta tropica*. Stable isotope data revealed a narrower isotopic niche and less intraspecific variation in trophic positions for Black-bellied Storm-petrels ($n = 15$) compared to Wilson's Storm-petrels ($n = 15$). GLS data suggested the non-breeding season of Wilson's Storm-petrels to last from around mid-April to end of November. All individuals ($n = 7$) migrated transequatorial in a clockwise pattern. Three individuals initially stayed at a non-breeding site in the South Atlantic Ocean. The main non-breeding sites of all individuals were in the North Atlantic Ocean, along the eastern coast of Canada and the United States, where flight feather moult took place from July to September, inferred from a period of reduced flight activity (measured by time on water). The foraging activity of Wilson's Storm-petrels was higher at night than during the day. This was not influenced by lunar phase but is likely linked to prey behaviour. The single successfully tracked Black-bellied Storm-petrel also crossed the equator but spent the non-breeding period in the Indian Ocean, mainly in the Arabian Sea. This indicates spatial segregation from Wilson's Storm-petrels. We present the first ever GLS tracking data of Wilson's and Black-bellied Storm-petrels, improving our understanding of their non-breeding behaviour. Future research including more individuals alongside environmental variables will be necessary to examine the drivers of the observed inter- and intraspecific non-breeding spatial and trophic segregation.

1 | Introduction

The annual cycle of seasonally reproducing animals, including many seabird species, comprises different life history events, such as reproduction, moult, and the non-breeding period. Throughout the annual cycle, prioritising varying life history events at different points of time, animals face a series of challenges during temporally and often spatially segregated reproductive and non-breeding periods (Marra et al. 2015; Dunn et al. 2020). In many breeding areas that

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experience seasonally adverse environmental conditions, such as the polar regions, migration is a common strategy for avoiding reduced food availability, prolonged periods of darkness, or adverse weather conditions (Cockell et al. 1999; Trouwborst 2013; Bestley et al. 2020).

Understanding the non-breeding ecology of seabird species is critical, as peak mortality typically occurs during this period, and many species reside in their non-breeding areas for more than half of their lifespan (Reynolds et al. 2011; Amélineau et al. 2021; Buckingham et al. 2022; Militão et al. 2022; Medrano, Hernández-Montoya, et al. 2024). Over the last decades, our understanding of the non-breeding distribution of large and medium-sized pelagic seabirds has steadily expanded through biologging (Amélineau et al. 2021; Beal et al. 2021; Bernard et al. 2021; Fauchald et al. 2021; Strøm et al. 2021). However, smaller, highly pelagic seabird species are among the least tracked species, and their non-breeding ecology remains largely unknown (Ausems et al. 2021; Bernard et al. 2021; Lambert and Fort 2022; Medrano, Hernández-Montoya, et al. 2024; Silva et al. 2024; Bolumar Roda et al. 2025; Wilkinson et al. 2025). These species are particularly challenging to study during the non-breeding period, as they are elusive and difficult to access somewhere out at sea, often covering vast distances (Warham 1992; Amélineau et al. 2021; Ausems et al. 2021; Militão et al. 2022; Medrano, Hernández-Montoya, et al. 2024). During the breeding season, however, they are constrained by offspring provisioning to a limited distance to their nest (Dunn et al. 2020; Militão et al. 2022). This can be taken advantage of by tagging individuals at their breeding site and subsequently tracking them during the non-breeding period (Fauchald et al. 2021).

Advances in the development of miniaturised and lightweight tracking devices enabled the tracking of smaller species (Maxwell et al. 2016; Lisovski et al. 2020; Strøm et al. 2021; Militão et al. 2022; Bolumar Roda et al. 2025). The use of light-level geolocators (also known as Global Location Sensors, GLS) has provided new and crucial knowledge on the ecology and conservation management of seabirds (Phillips et al. 2004; Tremblay et al. 2009; Rollinson et al. 2018; Redfern et al. 2021; Strøm et al. 2021; Militão et al. 2022). Many geolocator models have built-in conductivity recorders. This data can be used to determine whether the bird's leg was in contact with saltwater while resting or feeding (Militão et al. 2022). At-sea activity and moulting periods can then be inferred, as the proportion of time spent on the water usually increases during these periods (Cherel et al. 2016; Pastor-Prieto et al. 2019; Schoombie et al. 2022).

Either in complement to tracking data or on their own, stable isotope data can be used to study several aspects of the non-breeding ecology of seabirds (Jaeger et al. 2010; Weimerskirch et al. 2014; Cherel et al. 2016; Schoombie et al. 2022; Mills et al. 2024). The values of stable isotopes, most commonly carbon and nitrogen, in feathers (a metabolically inert tissue) can be used to infer the trophic position of seabirds and the rough latitudinal position at which they moult (Hobson 1990; Cherel et al. 2000; Jaeger et al. 2010; Quillfeldt, Thorn, et al. 2017). For example, in the Southern Ocean, it was validated that the well-defined latitudinal gradient in carbon isotopic values of particulate organic matter was found to be reflected in the tissue of consumers, so the values can be used to depict the foraging areas of petrels and albatrosses (Quillfeldt et al. 2010; Jaeger et al. 2010).

Compared to seabirds in temperate and equatorial regions, and to other Antarctic vertebrates such as penguins, pinnipeds and cetaceans, there is a paucity of literature on Antarctic flying seabird species (Ainley et al. 2012; Viola et al. 2023). Many of the flying seabirds in Antarctica belong to the order Procellariformes, which spend most of their time foraging at sea and come ashore only for breeding. Among them are the Wilson's Storm-petrel *Oceanites oceanicus*, the smallest endotherm that breeds in the Antarctic region (typically 35–45 g body mass; 15–20 cm total body length), and the slightly larger Black-bellied Storm-petrel *Fregetta tropica* (45–69 g; 18–22 cm; Thomas 2024).

Current data on the non-breeding distributions and migratory patterns of these two species are based on observations and a few stable isotope analyses. Field observations suggest that Wilson's Storm-petrels spend the austral winter in the North Atlantic, the Indian, and the Pacific Oceans, often crossing the equator (Harrisson 1983; Spear and Ainley 2007; Drucker et al. 2020). However, relatively little is known about their ecology during the non-breeding period (Gladbach et al. 2007; Ausems et al. 2021). The non-breeding distribution of Black-bellied Storm-petrels is also poorly understood (Ausems et al. 2021; Medrano and David 2023). It is assumed that they do not cross the equator, although they have been sporadically observed further north (Flood and Thomas 2007). Based on current knowledge from feather stable isotope values, it is hypothesised that, while breeding sympatrically, the two species moult and remain in different oceanic zones during the non-breeding period (Quillfeldt, Thorn, et al. 2017). Higher $\delta^{13}C$ and higher $\delta^{18}O$ values in Black-bellied Storm-petrels compared to Wilson's Storm-petrels indicate a more pelagic lifestyle and moulting grounds further north for Black-bellied Storm-petrels (Ausems et al. 2021). Feather stable isotope values of Wilson's Storm-petrels breeding on the South Shetland Islands predicted that some individuals moult < 44° S, that is, north of the Subtropical Front (Gladbach et al. 2007; Quillfeldt et al. 2005). Ausems et al. (2021) inferred from stable carbon and oxygen isotope values that most individuals moult in the temperate North Atlantic. However, different isotopic groups were suggested, with the Arctic being identified as an important moulting region for one group. The number of Wilson's Storm-petrels at King George Island has declined substantially (approx. 90% from 1978 to 2020). It is assumed that environmental conditions during the non-breeding period contribute to this decline. However, further studies into their non-breeding distribution are necessary to assess this (Ausems et al. 2023).

Neither Wilson's nor Black-bellied Storm-petrels have yet been tracked, due to the difficulty of deploying and recovering geolocators on such small and highly pelagic species. The objective of this study was to gain a first insight into their spatial ecology and pelagic activity patterns outside the breeding season. By combining geolocator data and feather stable carbon and nitrogen isotope values, we aimed to

TABLE 1 | Overview of recaptured storm-petrel individuals equipped with GLS logger.

No.	Sample ID	Species	Sex	Nest ID	Nest coordinates	Date GLS attachment	Date GLS recovery	End data recording light intensity	End data recording conductivity
1	WSP24_06	WSP	Male	N04	−62.2428, −58.6769	24.02.2023	30.12.2023	30.12.2023	30.12.2023
2	WSP24_07	WSP	Male	Y13	−62.2435, −58.6788	09.03.2023	30.12.2023	30.12.2023	30.12.2023
3	WSP24_08	WSP	Male	Y16	−62.2443, −58.6787	19.03.2023	30.12.2023	17.11.2023*	30.11.2023*
4	WSP24_09	WSP	Male	N24	−62.2448, −58.6791	15.02.2023	30.12.2023	30.12.2023	30.12.2023
5	WSP24_14	WSP	Male	N25	−62.2425, −58.6767	07.03.2023	05.01.2024	05.01.2024	05.01.2024
6	WSP24_24	WSP	Female	N86	−62.2435, −58.6790	14.03.2023	10.01.2024	18.12.2023*	22.12.2023*
7	BBSP24_17	BBSP	Male	N79	−62.2432, −58.6773	05.03.2023	16.02.2024	18.11.2023*	18.11.2023*
8	WSP23_11	WSP	Male	Y07	−62.2434, −58.6786	25.02.2023	17.01.2025	07.05.2024*	23.08.2024*

Note: Details of mounting and recapturing day as well as nest site, sex and GLS logging duration of Wilson's Storm-petrel *Oceanites oceanicus* (WSP) and Black-bellied Storm-petrel *Fregetta tropica* (BBSP) are given. GLS logger, which stopped data recording before GLS recovery, are marked with an asterisk (*) at the column 'end data recording'. All dates are denoted as dd.mm.yyyy.

I. Describe and compare their migratory phenology and flyways as well as non-breeding distribution.

II. Display at sea-activity patterns throughout the non-breeding period and check for differences in diurnal and nocturnal activity.

III. Identify timing and location of flight feather moult.

2 | Materials & Methods

2.1 | Bird Capture, Sampling & GLS Mounting

Wilson's Storm-petrels (subspecies: *O. o. exasperatus*, Clements et al. 2025, but see Norambuena et al. 2024) and Black-bellied Storm-petrels (*F. tropica*), both belonging to the austral storm-petrels (Oceanitidae, Pacha et al. 2023), were caught at a mixed breeding colony near the Argentine station 'Carlini' on King George Island/25 de Mayo Island, South Shetland Islands, within the ice-free area of the Potter Peninsula (62°14′ S, 58°40′ W). Birds were captured by hand at their nest burrows, which were located on the basaltic slopes of the old, eroded volcano 'Tres Hermanos' (Three Brothers Hill). Nests were checked from the end of January 2023 onwards, and adult birds with a chick (at least 14 days old) were chosen for GLS attachment. A total of 20 light-level geolocator (GLS) devices (INTIGEO-W30A9-SEA-NOT, 15 × 5 × 4 mm, ~0.45 g, Migrate Technology Ltd., Cambridge, UK) were deployed during the 2022/23 breeding season, 19 on Wilson's Storm-petrels and one on a Black-bellied Storm-petrel, as no other suitable nests were found for this species. This was probably due to the generally lower number of breeding pairs of this species (639–852) compared to Wilson's Storm-petrels (1400–2280) in the area (observed for breeding season 1995/96, Hahn et al. 1998). During our study, there were far fewer active nests following a 90% decline in Wilson's Storm-petrels (Ausems et al. 2023). However, no comparable data on population trends are available for Black-bellied Storm-petrels. In addition, Black-bellied Storm-petrel nests may be more difficult to detect. Beck and Brown (1971) already reported that Black-bellied Storm-petrel nests are well hidden and restricted to areas of consolidated scree composed of small boulders (approx. 20 cm in diameter), whereas Wilson's Storm-petrels nest in a wide variety of holes and crevices.

The GLS devices were attached by a cable tie, amalgamating tape and glue to an aluminium ring (diameter: 4–5 mm). The ring was placed above the tibio-tarsal articulation (total weight attachment material: ~0.35 g). The GLS devices and attachment material accounted for < 3% of the individuals' body weight (34.7–45.9 g for Wilson's Storm-petrels and 57.3 g for the Black-bellied Storm-petrel individual). Individuals were returned into their breeding burrows immediately afterwards. Eight individuals (recovery rate of 40%, Table 1) were recovered during consecutive breeding seasons (2023/2024 and 2024/2025) by repeatedly checking all known nest burrows of the colony (Table 1). All of the recovered individuals occupied the same nest as where they had been captured the first time.

For molecular sexing using the primer pair 2550F/2718R (Fridolfsson and Ellegren 2000, Supporting Information S1), a blood sample (~0.2 mL) was taken by puncturing the brachial wing vein with a cannula (⌀ 0.40 × 20 mm, B. Braun SE, Melsungen, Germany) and collected with heparinised capillaries (Vitrex Medical A/S, Herlev, Denmark). The samples were stored on FTA cards (Whatman, Buckinghamshire, UK).

At retrieval of birds in 2023 and 2024 (Table 1), we collected the entire outermost rectrices (R6) of each individual for stable isotope analysis. In addition to the individuals with GLS loggers ($n = 6$ Wilson's Storm-petrels and $n = 1$ Black-bellied Storm-petrels), we sampled adult individuals during nest checks or mistnet captures to increase the sample size for stable isotope analysis ($n = 15$ per species; Table S1). Both species moult their flight feathers outside of the breeding season (Beck and Brown 1972; Drucker et al. 2020; Ausems et al. 2021; Medrano and David 2023; Howell 2024), with rectrix feathers taking several weeks to grow (approx. 18 ± 3 days, Ausems et al. 2019). Rectrices generally moult distally, starting in the centre of the tail (R1 to R6), and it is assumed that rectrix moult overlaps to a considerable extent with the wing feather moult (Beck and Brown 1972; Ausems et al. 2021; Medrano and David 2023).

2.2 | Carbon and Nitrogen Bulk and Compound-Specific Stable Isotope Analysis

The R6 feather calamus was removed as this part of the shaft contains skin and blood residues. The feathers were placed in a tube and rinsed 3× in 96% ethanol and subsequently 4× with distilled water. Washing was enhanced by vortexing for 10 s for each rinse. Afterwards, the feathers were dried at 50°C for 48 h (Gordo 2020). Dried feather material from the inner and outer vane of the upper two-thirds (dark part of the R6) was cut into small fragments with stainless steel scissors (0.36 ± 0.11 mg) and weighed into tin cups (5 × 8 mm, IVA Analysetechnik GmbH & Co.KG, Meerbusch, Germany). These were then sent to the LIENSs laboratory (La Rochelle University, France).

Isotopic values were measured using a continuous-flow system consisting of an elemental analyser (Flash 2000, Thermo Scientific, Milan, Italy), equipped with the smart EA option and an autosampler (Zero Blank, Costech, Valencia, CA, USA), and connected via a Conflo IV peripheral to a Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). The uncertainty of the reported isotope-delta values was evaluated as the standard deviation of repeated ($n = 8$) measurements of reference material (USGS61 and USG63, US Geological Survey, Reston, VA, USA). Uncertainty of both δ^{13}C (^{13}C:^{12}C) and δ^{15}N (^{15}N:^{14}N) values did not exceed 0.10‰. Results are given in parts per thousand (‰) in the δ notation and were normalized using reference materials Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (Air-N_2) for carbon and nitrogen, respectively (cf. Quillfeldt et al. 2023).

Both isotope values were normally distributed (Shapiro Wilk test δ^{13}C: $W = 1.0$, $p = 0.400$; δ^{15}N: $W = 0.9$, $p = 0.059$). Since we did not detect significant differences between capture methods (mistnet vs. nest: Table S1, Welch two sample t-test δ^{13}C: $t = -0.2$, df = 12.0, $p = 0.871$; δ^{15}N: $t = 0.2$, df = 26.5, $p = 0.876$), between sample years 2023 and 2024 (δ^{13}C: $t = -0.3$, df = 25.7, $p = 0.794$; δ^{15}N: $t = -1.8$, df = 14.9, $p = 0.094$), and between female and male individuals (δ^{13}C: $t = 0.3$, df = 17.9, $p = 0.772$; δ^{15}N: $t = 1.5$, df = 24.5, $p = 0.154$), these sample groups were combined for further analyses.

To calculate species-specific isotopic niche widths, standard ellipse areas were calculated in R version 4.4.1 (R Core Team 2024). Standard ellipse areas (SEA) are used to represent the core isotopic niche width encompassing 40% of the data for each storm-petrel species, based on bivariate normal distributions (cf. Cherel et al. 2025). We calculated the corrected version of the standard ellipse area (SEAc) to account for the reduction in degrees of freedom when handling bivariate data and to adjust for small sample sizes (Jackson et al. 2011). The difference in SEAc between the species was evaluated through a bootstrapping approach (1000 bootstrap resamples), using the R package *boot* (Canty and Ripley 2024). The resulting distribution of interspecific SEAc differences provided a 95% confidence interval. Isotope data plots were generated using the R package *ggplot2* (Wickham 2016).

Compound-specific isotope analyses of amino acids (CSIA-AA) of R6 powdered feather samples (~9 mg, $n = 8$ Wilson's and $n = 7$ Black-bellied Storm-petrels) were performed at the UC Davis Stable Isotope facility, USA (described in Quillfeldt and Masello 2020). The mean standard deviation for sample replicates was ±0.16‰ and for reference material replicates ±0.27‰. Trophic positions (TP_{CSIA}) were calculated from the feather nitrogen stable isotope values of glutamic acid (Glx) and phenylalanine (Phe), using a stepwise trophic discrimination factor (Quillfeldt and Masello 2020; Thébault et al. 2021 for a detailed description) with the following equation:

$$TP_{CSIA} = 2.0 + \frac{\text{Glx} - \text{Phe} - 3.5\,‰ - 3.4\,‰}{6.2\,‰}$$

To calculate the trophic positions of all feather samples ($n = 39$), using their bulk stable isotope values, we followed the approach of a linear regression model to examine the relationship between TP_{CSIA} and bulk stable isotope values (δ^{13}C and δ^{15}N), as described in Thébault et al. (2021). However, as the model showed no significant relationship (Adjusted $R^2 = 0.21$, $F_{2,12} = 2.9$, $p = 0.094$), we only used the data of the CSIA-AA to derive trophic positions (TP_{CSIA}). TP values were not normally distributed (Shapiro Wilk test $W = 0.9$, $p = 0.021$) and thus compared between species with a Wilcoxon rank sum test.

2.3 | GLS Data Analysis

Geolocators record and store solar irradiance (ambient light), enabling the estimation of positions of tracked individuals (Wilson et al. 1992; Hill 1994). The registered light data is used to determine day length and the time of solar noon, allowing latitude and longitude, respectively, to be estimated with an average accuracy of around 200 km (Phillips et al. 2004; Fudickar et al. 2011; Merkel et al. 2016). The GLS loggers we used were set to UTC time and had two types of sensors: light (used for geolocation) and conductivity (wet/dry, i.e., immersion in saltwater, used for activity). Light intensity (0.320–74,000 lx) was sampled every minute, with the maximum value recorded within each 5-min period. Saltwater immersion check was performed every 30 s, with the number of samples classified as 'wet' (conductivity > 63) being recorded every 10 min. This resulted in values ranging from 0 to 20. These settings correspond to the manufacturer (Migrate Technology Ltd) mode 'W30-6'. After logger retrieval, the raw data were downloaded using IntigeoIF v1.15 software (Migrate Technology Ltd., Cambridge, UK). Two geolocators (Bird IDs: BBSP24_17 and WSP23_11, Table 1) had to be sent to the manufacturer for data download.

2.3.1 | Processing of Light Intensity Values — Geolocation Data

Subsequent data preparation and coordinate extraction were conducted in the statistical programming software R, version 4.4.1 (R Core Team 2024). Following Lisovski et al. (2020), we converted light-level geolocator data into geographic locations using the threshold method of twilight estimation. This is built on the principle that locations can be determined based on known temporal variation of solar noon and day length across the earth (Hill 1994; Hill and Braun 2001; Ekstrom 2004). We defined twilights using a light threshold value of three within the function 'preprocessLight' in the R package *TwGeos* (Lisovski et al. 2016). Outliers of twilight estimates, defined as > 60 min earlier or later than the four neighbouring twilights, attributed to shading events (e.g., caused by a combination of weather, topography, or vegetation; Lisovski et al. 2012), were automatically edited or removed using the 'twilightEdit' function in *TwGeos*.

Subsequently, we used probabilistic modelling via Markov Chain Monte Carlo (MCMC) as implemented in the R package *SGAT* (Solar/Satellite Geolocation for Animal Tracking, Sumner et al. 2009; Lisovski and Hahn 2012). A site-specific calibration, lasting 11 ± 5 days, was chosen for each individual at the deployment location at the colony (62.24° S, 58.67° W) in order to estimate the zenith angle. The median zenith angles for individuals ranged from 92.1° to 96.0° (mean 94.6 ± 1.3°). A gamma distribution was used to model uncertainty in twilight transitions. Initial positions were estimated using a threshold method with the *SGAT* function 'thresholdPath' and then refined through Bayesian state-space modelling (function 'thresholdModel'). The MCMC estimation was performed using the 'estelleMetropolis' function. The model was run in several sequential fitting phases, each consisting of 900 to 1000 iterations with thinning every 20 steps. The final position estimates and associated 95% credible intervals were extracted using the 'locationSummary' function.

The number of position estimates (two per day) varied from 480 to 575 per individual, depending on the battery lifetime of the GLS logger and the start of breeding burrow visits, which caused disturbed light intensity records. Further filtering removed position estimates with a standard deviation of more than 30 (3.5% of all position estimates). High deviations often occurred around equinox periods (equinox ±14 days; for the tracking year 2023: 6 March to 3 April and 9 September to 7 October). In graphical representations, position estimates falling within the autumnal and vernal equinox periods were included, but clearly marked, acknowledging that geolocation is less reliable during these times due to equal day lengths across latitudes (Phillips et al. 2004; Schoombie et al. 2022).

To account for the pelagic lifestyle of storm-petrels, we incorporated a land–sea mask derived from the Natural Earth database (via the R package *rnaturalearth*, Massicotte and South 2023). The mask was used to assign position estimates as either 'land' or 'sea'. Subsequently, positions falling on land were corrected by shifting them longitudinally towards the coast of previous estimates until a sea location was reached. After these filtering steps, all location estimates were visually examined in a geographical information system (QGIS 3.34 Prizren, QGIS Development Team 2023), and any unrealistic positions remaining, such as sudden long-distance movements over a short time, that is, unrealistic speed, which were associated with interference to light curves at dawn or dusk or in temporal proximity to equinoxes, were filtered out (Quillfeldt et al. 2015, 2019).

Generally, we considered the non-breeding period to span from the day after the last positions in the colony surroundings until the first visit of a nest burrow in the colony (cf. Militão et al. 2022). More precisely, the onset of northward migration (from breeding grounds to non-breeding sites) was set if an individual moved at least 250 km away from the breeding colony, did not return to the colony location and surrounding sea, and exhibited a directed flight (for all Wilson's Storm-petrels in direction to the South Atlantic Ocean). The 250 km represents the estimated foraging range of Wilson's Storm-petrels around their colony (Croxall and Prince 1980; Pennycuick et al. 1984). Non-breeding sites were assumed when an individual remained rather stationary (daily movements within approx. ±250 km, repeating use of locations) in a specific area for at least 14 consecutive days.

Some individuals performed movements before the start of their southward migration, that is, pre-migratory movements. These were defined as sustained flight movements in a larger radius than in the non-breeding sites, but without a directed southern direction (unlike migration). Southward migration, back to the breeding site, was defined as the departure from non-breeding sites in a southward directed flight without any return movements. The beginning of the breeding season was determined by an individual's arrival in the breeding colony area, accompanied by nest burrow visits, indicated by light-level data.

2.3.2 | Kernel Utilization Distribution of Non-Breeding Sites

Individual non-breeding site distributions (i.e., kernel utilization distribution, short KUD) were extracted using the 'kernelUD' function within the R package *adehabitatHR* (Calenge and Fortmann-Roe 2023), with a smoothing factor h of 2°, a bivariate normal kernel, a grid size of 500, and an extent of 2.

This analysis was performed for each individual bird for all locations within the non-breeding stage and per site, as defined by visual inspection in QGIS. A smoothing factor of 2° was chosen as this value aligns with the accuracy of location estimations derived from geolocators (cf. Schoombie et al. 2022). The 50% and 95%-KUDs (i.e., core areas and non-breeding home ranges) were visualised on a map alongside migration tracks and pre-migratory movements in QGIS, using the WGS84 coordinate reference system (EPSG: 3857). To remove terrestrial overlap from the KUDs, a spatial difference operation was performed in QGIS, resulting in a distribution constrained to oceanic areas. The 'st_area' function in R package *sf* (Pebesma 2018; Pebesma and Bivand 2023) was used to estimate the area in km^2 of the 50% and 95% KUDs. We then applied the 'st_intersection' function to quantify the degree of overlap, if present, between the KUDs of individual Wilson's Storm-petrels.

2.3.3 | Processing of Conductivity Data — Activity Patterns

The daily proportions of time spent on the water, which was interpreted as resting behaviour, were assessed based on the wet-dry data collected every 30 s and stored as 10-min interval data. We assumed that the geolocators were immersed in saltwater when a bird was resting and/or preening on the ocean surface, that is, this behaviour was associated with prolonged 'wet' activity (cf. Cherel et al. 2016; Viola et al. 2023). The loggers likely dried quickly once a bird became airborne (flying behaviour).

Following Cherel et al. (2016), we used the daily variation in the proportion of time spent sitting on the water to determine when the individuals most likely moulted their flight feathers. For this purpose, we totalled the number of hours spent on the water and calculated the daily average time spent on water per individual. Individual-based estimates of moult timing were based upon a generalised additive model (GAM) fitted to the 'wet' data for each bird's annual cycle (Cherel et al. 2016; Grissot et al. 2020). The core moult period was defined as the period (consecutive days) when the predicted 'wet' variable exceeded 75% of the value of the peak in the daily proportion of time wet (Figure S1). These GAM results provided estimates of the start and end dates and duration of the core moult period.

Subsequently, we separated the activity data into day and night according to sunrise and sunset times of the corresponding calculated position estimate with the 'sunrise.set' function in the R package *StreamMetabolism* (Sefick 2023). Additionally, the function 'lunar.phase' (R package *lunar*, Lazaridis 2022) assigned these points to a moon phase (grouped radian value: 0—new, $\pi/2$—waxing, π—full and $3\pi/2$—waning moon phase, cf. Schoombie et al. 2022).

To check whether the proportion of time spent on water differs between day and night, we used a generalised linear mixed-effects model (GLMM, R package *glmmTMB*, Brooks et al. 2017; McGillycuddy et al. 2025) with categorical levels 'day' and 'night' as a fixed effect predictor and individual bird identity ($n=7$ Wilson's Storm-petrels) as a random intercept. In this analysis, we excluded the one Black-bellied Storm-petrel due to the small sample size in order to avoid mixing potential species-specific patterns. To examine the possible effect of the moon phase on the proportion of time spent on water, we ran another GLMM on night data only, with moon phase as a fixed effect and bird identity as random intercept. Post hoc pairwise comparisons between moon phases were performed using Tukey-adjusted estimated marginal means to identify differences among the phases.

2.4 | Linking Bulk Stable Isotope and Geolocator Position Estimates

For six Wilson's Storm-petrels equipped with GLS (Table S1), we have results for nitrogen and carbon isotope values of R6 feathers grown during the non-breeding season when the GLS data was collected. Following an initial visual inspection of scatter plots (Figure S2), linear regression analyses were performed using δ^{13}C and δ^{15}N values as response variables, in order to assess the association between stable isotope values and moulting location (mean moulting latitudes and longitudes as estimates from GLS data, Table 2). Individual moulting latitude and longitude were included as continuous predictor variables in two separate linear regression models.

3 | Results

3.1 | Stable Isotope Niches and Trophic Positions

The mean feather δ^{13}C was −18.0‰ ± 0.3‰ for Black-bellied Storm-petrels and −18.5‰ ± 1.6‰ for Wilson's Storm-petrels. For δ^{15}N means were 13.7‰ ± 0.7‰ for Black-bellied Storm-petrels and 13.8‰ ± 0.5‰ for Wilson's Storm-petrels (Figure 1). There was no interspecific significant difference in the carbon and nitrogen isotope values (Welch two sample *t*-test δ^{13}C: $t=1.6$, df = 14.7, $p=0.226$; δ^{15}N: $t=-0.4$, df = 24.6, $p=0.700$). However, the SEAc for Black-bellied Storm-petrels (SEAc = 0.64) was significantly smaller, that is, they have a narrower isotopic niche, compared to Wilson's Storm-petrels (SEAc = 2.27; Figure S3), with a mean difference estimated via bootstrapping of −1.45 (95% confidence interval: −2.28 to −0.55). The mean TP_{CSIA} for Black-bellied Storm-petrels ($n=7$) was 3.8 ± 0.1 (3.6 to 4.0) and slightly higher than the trophic position of Wilson's Storm-petrels ($n=8$, TP_{CSIA}: 3.4 ± 0.5, 2.8–4.1), though the interspecific difference was not significant (Wilcoxon rank sum test W = 37.5, $p=0.292$).

3.2 | Temporal Pattern of the Non-Breeding Period

The non-breeding period, starting with the onset of northward migration and ending with the beginning of the breeding season, for Wilson's Storm-petrels on average started on 10 April (24 March–18 April) and ended on the 28 November (22 November–11 December, Figure 2, Table S2). The non-breeding period thus lasted between 219 and 262 days (mean 233 ± 15 days). The only individual (WSP_Y07) whose chick died before fledging, after a snow blockage, left the breeding site the earliest and as only one in March (Table S2). Returning to their breeding areas after southward migration, Wilson's Storm-petrels visited a nesting burrow for the first time on 28 November ±7 days (Table S2). For the one tracked Black-bellied Storm-petrel, no reliable information on start and end of the non-breeding period can be provided based on available light intensity data (Table S2).

TABLE 2 | Estimated core moult period of flight feathers of Wilson's Storm-petrels (WSP) and Black-bellied Storm-petrels (BBSP).

Bird ID	Species	Start of moult	End of moult	Duration [days]	Core moult location	Moult mean Lon ± SD	Moult mean Lat ± SD
N86	WSP	30.06.2023	01.09.2023	64	Gulf of St. Lawrence, Gulf of Maine, Labrador Sea	−67.98 ± 20.34	45.79 ± 13.90
N25	WSP	04.07.2023	25.08.2023	53	Grand Banks of Newfoundland	−50.70 ± 2.74	45.22 ± 2.04
Y16	WSP	06.07.2023	26.08.2023	52	Gulf of Maine	−69.27 ± 23.12	43.59 ± 14.58
N24	WSP	06.07.2023	08.09.2023	65	Grand Banks of Newfoundland, Labrador Sea	−47.48 ± 1.97	45.17 ± 3.48
N04	WSP	07.07.2023	26.08.2023	51	Grand Banks of Newfoundland, Gulf of St. Lawrence	−54.50 ± 2.40	46.45 ± 2.73
Y07	WSP	12.07.2023	04.10.2023	85	Gulf of St. Lawrence, Gulf of Maine	−67.54 ± 13.38	42.90 ± 14.85
Y13	WSP	25.07.2023	03.10.2023	71	Gulf of St. Lawrence, Labrador Sea	−62.85 ± 19.80	50.31 ± 16.27
N79	BBSP	29.08.2023	23.10.2023	56	Southwestern Indian Ocean	44.94 ± 18.87	−26.66 ± 29.56

Note: Individual-based estimates of the moult timing based upon a generalized additive model (GAM) that was fitted to the collected 'wet' immersion data. Core moult period was defined as the time (several consecutive days) when the predicted 'wet' variable exceeded 75% of the value of the peak in the daily proportion of time wet (see Figure S3 for individual plots). The GAM results provided estimates of the start and end dates of the moult, given here as dd.mm.yyyy with respective duration and moult location estimates (Figure S4) based on processed geolocator light intensity values (Lon = Longitude, Lat = Latitude).

3.3 | Migration Patterns and Non-Breeding Period Distribution

While the Black-bellied Storm-petrel had one non-breeding site in the Indian Ocean (Figures 2 and 3), more precisely the Arabian Sea, Gulf of Oman and the Persian Gulf, Wilson's Storm-petrels spent the non-breeding time in the Atlantic Ocean. Three of the seven Wilson's Storm-petrels used two distinct non-breeding sites. These three individuals, before crossing the equator, first occupied a non-breeding site in the South Atlantic Ocean at the eastern coast of South America (Figure 3a), where they were for 28 ± 12 days (Figure 2, Table S2). All seven Wilson's Storm-petrels had non-breeding sites in the North Atlantic Ocean, at the eastern coast of the USA and Canada, with core areas around Maine, Nova Scotia, Prince Edward Island and Newfoundland (Figures 3 and S4), with centroids of 50% KUDs ranging roughly from longitude −69° to −52° and latitude 41°to 45° (Figure 2, Table S3). At first, all 50% KUDs in the North Atlantic Ocean of individuals were located rather close to the coast; for three individuals, the 50% KUDs were shifted, with progressing non-breeding time, to areas further away from the coast (Figures 3 and S4), resulting in varying overlap from 0% to 89% of the KUDs of individuals (Table S4). At North Atlantic non-breeding sites, Wilson's Storm-petrels spent 115 ± 24 days, ranging from 11 May until 14 October (Table S2). 50% KUDs in the North Atlantic Ocean ($n = 7$) had a size of 314,898 ± 137,717 km^2, compared to 298,075 ± 69,317 km^2 for 50% KUDs in the South Atlantic Ocean ($n = 3$) and 739,216 km^2 for the Black-bellied Storm-petrel in the Indian Ocean (Table S3).

Prior to the onset of southward migration, all Wilson's Storm-petrels performed pre-migratory movements (Figure 2) with varying locations, for example, leading as far north as Iceland (WSP_N04) or into the Caribbean Sea (WSP_Y07, Figure 3b). Southward migration started on 10 October ±15 days (Table S2). While northward migration mainly followed the South American coastline, southward migration paths often extended further eastward, reaching the West-African coast, before crossing the Atlantic Ocean to reach areas closer to the East-coast of South America (Figure 3b). The mean duration of the southward migration was 51 ± 15 days ($n = 5$). This was longer than the northward migration, which lasted 30 ± 5 days for birds ($n = 4$) with only one non-breeding site in the North Atlantic, or 6 ± 2 days for individuals ($n = 3$) first flying to non-breeding sites in the South Atlantic Ocean, followed by further 21 ± 8 days to reach their North Atlantic non-breeding sites.

3.4 | Activity Data and Moulting Areas

Analysing the proportion of time spent on the water, that is, resting or preening behaviour on the ocean surface, revealed main changes on activity, namely an increased proportion of the time spent on water, starting in June and lasting throughout October (Figure 4). Based on the variation in time spent on water the core moulting period of flight feathers for Wilson's Storm-petrels was determined from 8 July to 11 September (Figure 4) with slight variations in timing for individual birds (Table 2, Figure S1). The moult period of the one Black-bellied Storm-petrel was calculated for later in the year, from 29 August until 23 October (Table 2, Figure S1). In Wilson's Storm-petrels, the increase in time on water, most likely resting behaviour, was particularly

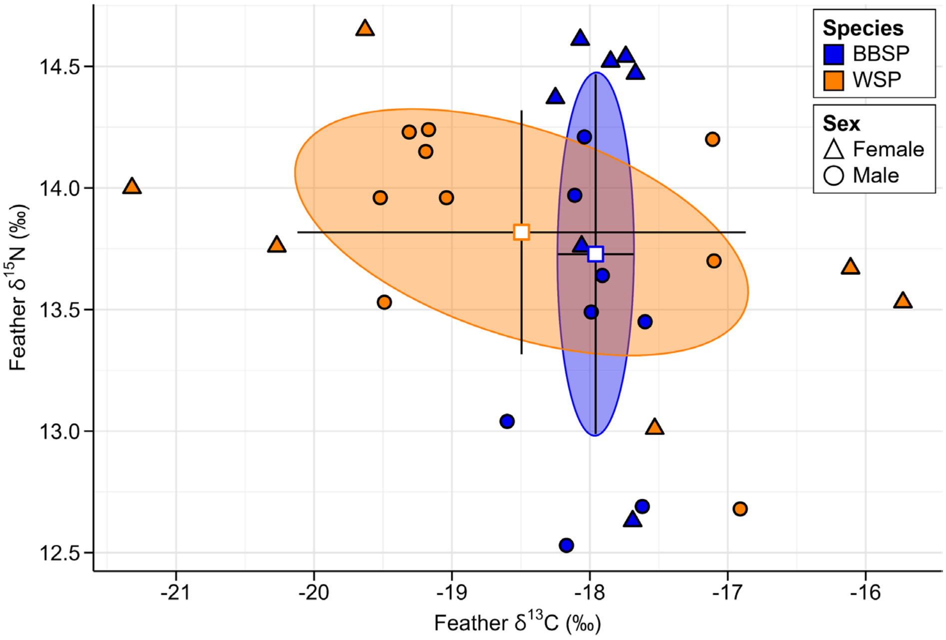

FIGURE 1 | Biplot of R6-feather (outermost rectrix) stable isotope values (‰) of carbon (δ^{13}C) and nitrogen (δ^{15}N) for individual male and female Black-bellied Storm-petrels *Fregetta tropica* (BBSP, blue, $n = 15$) and Wilson's Storm-petrels *Oceanites oceanicus* (WSP, orange, $n = 15$), sampled on King George Island. White squares are mean ± SD δ^{13}C and δ^{15}N values per species. Solid lines depict standard ellipse area (SEAc, approx. 40% of the data).

pronounced during the day (Figure 4). The GLMM revealed a significant effect of time of day on the proportion of time spent on water ('wet' counts). The proportion of resting behaviour was lower during the night compared to the day with 5.6% ± 8.6% and 24.1% ± 22.0%, respectively (GLMM: estimate $= -0.95$, SE $= 0.03$, $z = -27.28$, $p < 0.001$; Table S5 for individual values). Post hoc pairwise comparisons between moon phases revealed no significant differences in time spent on water during the night (Table 3), that is, no link of resting behaviour to moon phase.

All Wilson's Storm-petrels moulted in the North Atlantic Ocean. The core moult locations were in the Gulf of St. Lawrence, the Gulf of Maine, the Labrador Sea, and the Grand Banks of Newfoundland (Table 2, Figure S5). The Black-bellied Storm-petrel moulted in the Indian Ocean, moving southwards from the Gulf of Oman to more pelagic areas of the Southwestern Indian Ocean (Figure S5).

3.5 | Relationship of GLS Estimates and Stable Isotope Values

Linear regression revealed a significant relationship between Wilson's Storm-petrel δ^{13}C values and moulting location ($R^2 = 0.87$, $F_{2,3} = 9.7$, $p = 0.049$). Longitude was a significant predictor (estimate $= -0.11$, $p = 0.024$), indicating that δ^{13}C values increased with a more westerly position. Latitude did not significantly influence δ^{13}C values ($p = 0.380$). The regression model for δ^{15}N values was not statistically significant ($R^2 = 0.50$, $F_{2,3} = 1.5$, $p = 0.359$). Neither longitude ($p = 0.255$) nor latitude ($p = 0.376$) significantly predicted nitrogen isotopic values. Due to the small sample size ($n = 6$ Wilson's Storm-petrels), further statistical analyses were not performed, nor were the results of the linear regression used to predict moulting locations for further individuals based solely on their feather stable isotope values.

4 | Discussion

Outside their breeding season, it is particularly challenging to study small, pelagic seabirds as they are widely dispersed somewhere at sea (Quillfeldt, Engler, et al. 2017; Ausems et al. 2019; Militão et al. 2022; Medrano, Hernández-Montoya, et al. 2024). However, it is a crucial period in their life cycle as they undergo the challenging phases of migration and flight feather moult. They can be particularly vulnerable during this time (Hedenström and Sunada 1999; Trull et al. 2018; Hedenström 2023). To obtain spatial and activity data during the non-breeding season and infer when and where flight feather moult occurs, we combined light-level immersion geolocators and stable isotope analysis. Although position estimates via GLS logger are less accurate than GPS positions (Phillips et al. 2004; Fudickar et al. 2011; Merkel et al. 2016), they provide us a coarse indication of distribution throughout the entire non-breeding period without being limited by battery capacity. This level of temporal coverage is currently unachievable with lightweight GPS devices due to their limited battery life. Since the two species have never been tracked before, our results considerably broaden our understanding of their non-breeding ecology, particularly with regard to their distribution.

4.1 | Wilson's Storm-Petrel: Non-Breeding Distribution, Migration and Moult

Earlier research on Wilson's Storm-petrels, based on feather stable isotope data, suggested that individuals spending the non-breeding period in the Northern hemisphere are mainly pre-breeders. While adult breeding birds use the South Atlantic at the Subtropical Front, with most expected to moult around latitude 51° S (Quillfeldt et al. 2005; Gladbach

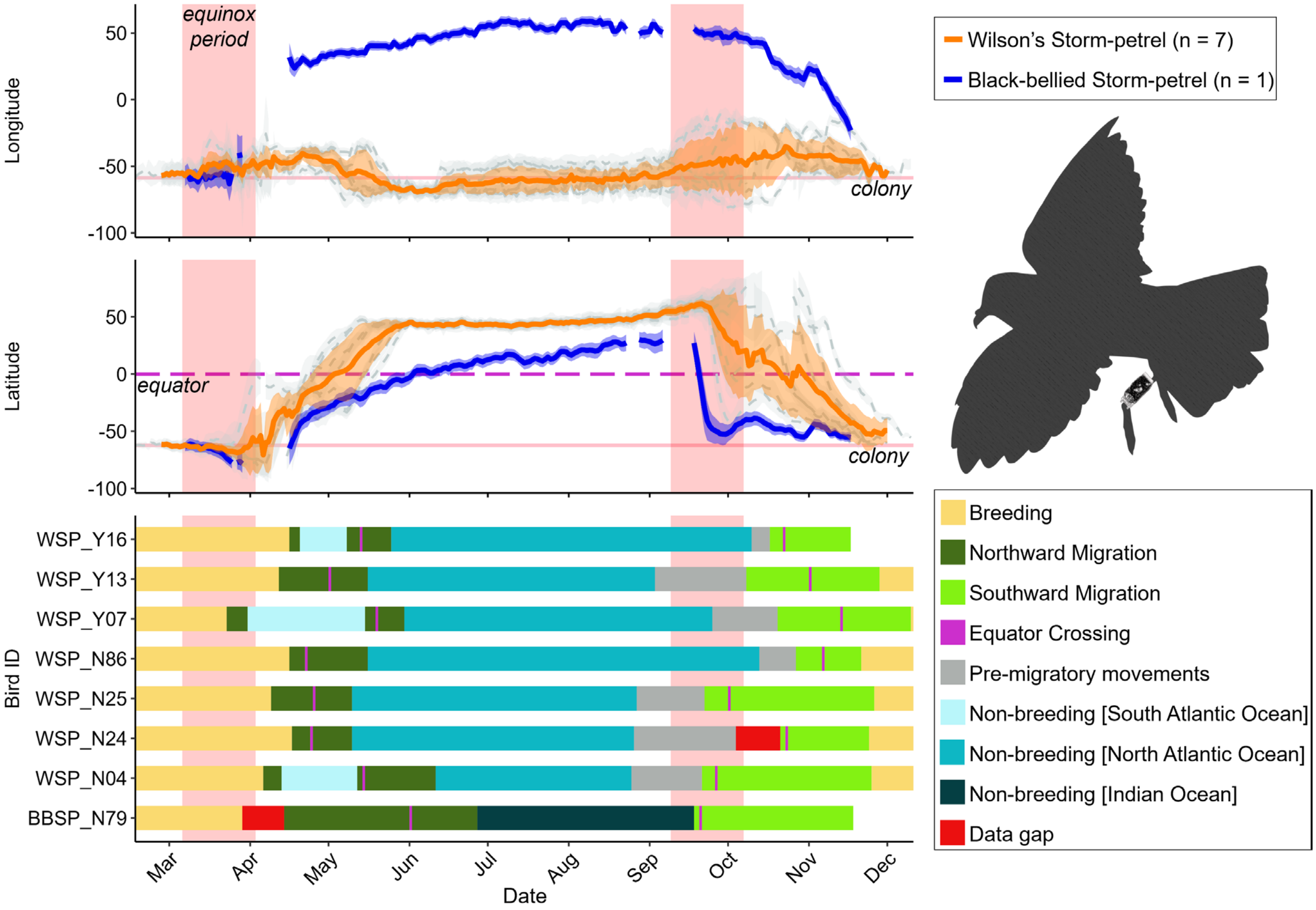

FIGURE 2 | Annual phenology of Wilson's Storm-petrels *Oceanites oceanicus* (WSP) and Black-bellied Storm-petrels *Fregetta tropica* (BBSP) based on the geographical location estimates obtained from geolocators. Mean longitudes (top) and mean latitudes (middle) are shown as lines with standard deviation (shaded areas) as mean for the seven tracked Wilson's Storm-petrel individuals (orange line) and the one tracked Black-bellied Storm-petrel (blue line). Latitudinal and longitudinal estimates of each Wilson's Storm-petrel individuum are shown in dashed grey lines. If the solid or dashed lines are interrupted, no reliable position estimates were obtained. The breeding colony longitudinal and latitudinal position is presented as pink line and the equator as dashed pink line. Equinox periods of the year 2023 are shaded in red. Chronology of the different phenological stages (for definitions of stages see description in the main text) is expressed as one horizontal bar for each bird (bottom). Time scale starts with GLS logger deployment of the first individual (16th of February 2023) and extends until the last individual visits a breeding burrow for the first time (11th of December 2023). For individuals WSP_Y16 and BBSP_N79 light sensors stopped logging during their southward migration.

et al. 2007). Three out of seven of our tracked Wilson's Storm-petrels (all breeding adults) first had a non-breeding site in the South Atlantic, along the east coast of South America. All tracked individuals had their main non-breeding site in the North Atlantic, around Nova Scotia and Newfoundland. Our tracking data thus establish a direct link between a particular breeding colony on King George Island and non-breeding areas in the North Atlantic. This provides confirmed information on the subspecific identity of Wilson's Storm-petrels, namely *O. o. exasperatus*, present in the North Atlantic. Our analyses also identified these areas as the core moulting areas. The difference in non-breeding areas predicted by stable isotopes may be due to similar stable isotope values in temperate to subpolar marine areas in both hemispheres. However, this clearly needs to be verified with a larger sample size, particularly since we could only find a significant relationship between feather $\delta^{13}C$ values and moult longitude estimation (increase with a more westerly position), but not with latitude. Ausems et al. (2021) used stable isotope analysis to construct a distribution prediction model for Wilson's Storm-petrels sampled at another breeding colony on King George Island. Consistent with our findings, this study suggested the same areas around Nova Scotia and the Labrador Sea as potential moulting locations.

The migration routes of Wilson's Storm-petrels are rarely described in literature, and existing descriptions are often incomplete. The continental shelf 10 km east of Chatham, Massachusetts, is mentioned as a known corridor for northward migration (Trull et al. 2018). Other studies described that they migrate north mainly over the continental shelf on the western side of the North Atlantic (Brown 1986; Nisbet et al. 2013). They are reported to migrate north along both sides of the Atlantic, though mainly along the western side, but allegedly not through the central Atlantic (Flood and Thomas 2007). Nisbet et al. (2013) state that the southward migration is undocumented. Our tracked individuals were all transequatorial migrants, flying for northward migration mainly along the continental shelf on the western side of the North Atlantic, along the eastern coasts of South and North America.

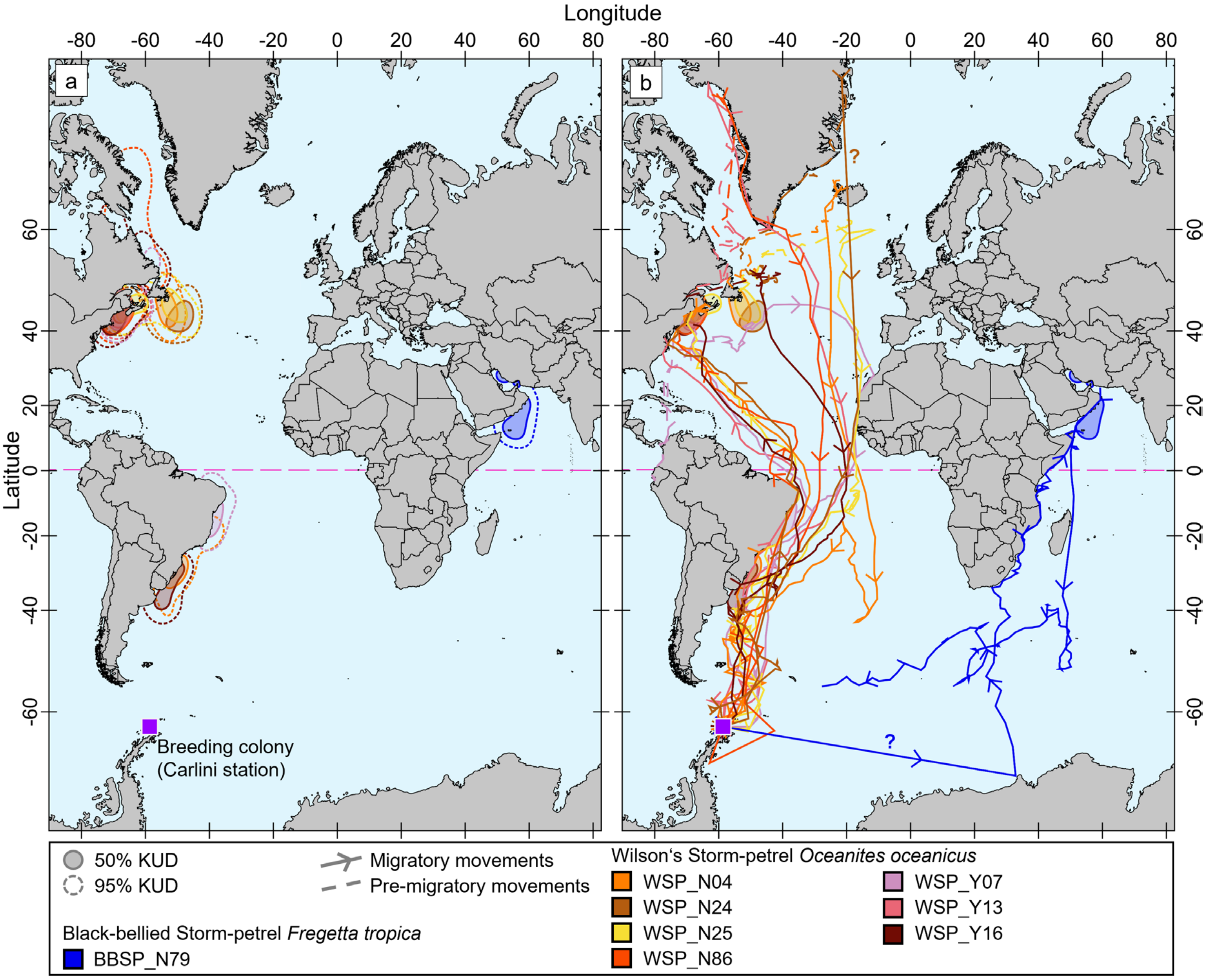

FIGURE 3 | Non-breeding distribution of the seven Wilson's Storm-petrels *Oceanites oceanicus* (WSP, orange-tones) and the one Black-bellied Storm-petrel *Fregetta tropica* (BBSP, blue) with a geolocator. The purple square indicates the location of the breeding colony of the tracked birds on King George Island. The pink dashed line represents the equator. (a) The filled areas represent the 50% kernel utilization distribution (KUD) and the dotted line the 95% KUD of individual non-breeding sites. Zoomed in kernels of the Wilson's Storm-petrels in the North Atlantic Ocean can be viewed in Figure S2. (b) Besides the 50% KUDs, the migratory movements (solid lines) are shown for each individual. Arrows on lines indicate flight direction. Dashed lines represent pre-migratory movements before onset of southward migration. For two birds longer-term data gaps existed (WSP_N24: 4th October to 21st October and BBSP_N79: 29th March to 14th of April) and are marked with a coloured question mark.

After leaving their non-breeding sites in the North Atlantic Ocean, all seven individuals performed pre-migratory movements, with variation in duration and location. However, there was no clear pattern in terms of the start of the pre-migratory movements and the end of the moult. The birds may have followed shifts in the location of prey or wind, but our dataset cannot answer this question and further research is needed. Generally, migration routes of Wilson's Storm-petrels were clockwise in the North Atlantic. Their southward migration started further east, with most individuals reaching the west coast of Africa before crossing the Atlantic Ocean. They then migrated towards the colony along the East coast of Brazil and through the Argentine basin. This migration route fits within the Atlantic Ocean flyway, which is described as one out of six global flyways for migratory pelagic seabirds (Morten et al. 2025). The loop in the North Atlantic is also present in this description of this flyway. Some South Polar Skuas *Catharacta maccormicki*, breeding on King George Island, followed similar migration routes, at least in broad terms, as the Wilson's Storm-petrels (Kopp et al. 2011). In particular, the crossing of the Atlantic Ocean during southward migration was notably similar. The flyway is likely chosen as it corresponds with major wind-driven ocean currents (Morten et al. 2025).

The arrival time of our tracked individuals back at the colony in mainly November fits with some arrival times given in literature for adults returning to Signy Island and South Orkney Islands (Beck and Brown 1972) as well as to other islands and the Antarctic continent (summarized in Wasilewski 1986).

4.2 | Black-Bellied Storm-Petrel: Non-Breeding Distribution, Migration and Moult

The one tracked Black-bellied Storm-petrel individual was also a transequatorial migrant, but its non-breeding site was much further east and south than those of Wilson's Storm-petrels. It was located in the Arabian Sea, more precisely in the Persian

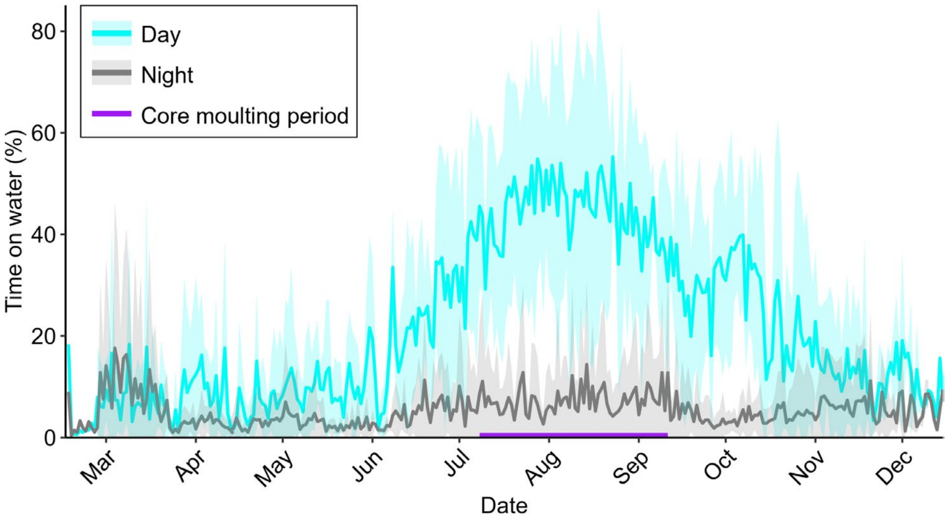

FIGURE 4 | Daily average (±SD, shaded area) of the time spent on water (%, 'wet' counts of conductivity, i.e., immersion data) for Wilson's Storm-petrels *Oceanites oceanicus* ($n = 7$), split for day (turquoise line) and nighttime (grey line), mainly spanning the non-breeding period. The core moulting period of flight feathers is indicated by the purple line. All data is from birds equipped with geolocators within the year 2023.

TABLE 3 | Pairwise post hoc comparisons of moon phase effects on the proportion of time spent on water by Wilson's Storm-petrels *Oceanites oceanicus* during night (sunset to sunrise data points), based on a beta regression GLMM with individual birds (Bird ID) as a random effect.

Moon phase pairs	Estimate	SE	*z* ratio	*p*
Full—New	−0.0045	0.0614	−0.073	0.999
Full—Waning	−0.1242	0.0609	−2.039	0.174
Full—Waxing	−0.0438	0.0609	−0.720	0.890
New—Waning	−0.1197	0.0612	−1.955	0.205
New—Waxing	−0.0393	0.0611	−0.643	0.918
Waning—Waxing	0.0804	0.0607	1.324	0.548

Note: Estimates are given on the log odds scale, and *p* values are adjusted using Tukey's method.

Gulf and the Gulf of Oman in the Indian Ocean. During moult, the bird moved to more pelagic areas closer to the Southern Indian Ocean Island. Flood and Thomas (2007) report that the northward movement of Black-bellied Storm-petrels from their colonies occurs from April to May, with the birds dispersing into tropical and subtropical seas as far north as 10° N in the Atlantic before returning from September to November. This fits with the observed phenology of our tracked individual, although its wintering site was located further north. The distribution prediction model in Ausems et al. (2021) showed a high probability of origin for Black-bellied Storm-petrels feathers in the Arabian Sea, around Oman, Yemen and Somalia. This is in accordance with the wintering area of our tracked individual. Clearly, results from just one individual provide limited insight into the non-breeding distribution of the species. However, it is an important first step because the non-breeding distribution of Black-bellied Storm-petrels is still largely understudied (Ausems et al. 2021; Medrano and David 2023).

4.3 | Non-Breeding Activity and Foraging Patterns

Our results indicate a diel pattern in wet time, with Wilson's Storm-petrels spending more time on the water during the day. Both species show nocturnal behaviour during the breeding season (Croxall et al. 1988; Warham 1992; Hahn 2000; Quillfeldt and Möstl 2003; Jouventin et al. 2007). During the non-breeding period, our results indicate that Wilson's Storm-petrels were more active at night than during the day, spending less time resting on the water and more time flying, for example, to search for prey. In breeding areas, storm-petrels are nocturnal likely to avoid excessive predation by avian predators (Warham 1992; McNeil et al. 1993; Madani 2020). However, Wilson's Storm-petrels' usually maintain their diel rhythm during the 24-h daylight period in the breeding areas (Jouventin pers. obs. in Jouventin et al. 2007). Our results suggest that nocturnal activity, most likely foraging activity, is also predominant during the non-breeding season.

Higher night-time activity throughout the non-breeding season was also observed in other storm-petrel species, such as the European Storm-petrel *Hydrobates pelagicus* (Militão et al. 2022), White-faced Storm-petrel *Pelagodroma marina* (Medrano, Repullés, et al. 2024), Townsend's Storm-petrel *H. socorroensis*, and Ainley's Storm-petrels *H. cheimomnestes* (Medrano, Hernández-Montoya, et al. 2024). Likewise, similar to other storm-petrel species, for example, European Storm-petrel (Militão et al. 2022) and the Cape Verde Storm-petrel (*H. jabejabe*; Medrano et al. 2022), we found no significant influence of the moon phase on the night activity of Wilson's storm-petrels throughout the non-breeding season.

The active foraging behaviour in the night is most likely related to the diel vertical migration of the storm-petrels zooplanktonic and small fish prey, so that the prey is closer to the sea surface at night than during the day, making it accessible for storm-petrels (Croxall et al. 1988; Hays 2003; Hedd et al. 2009; Watanuki and Thiebot 2018; Medrano, Repullés, et al. 2024; Silva et al. 2024). As the GLS loggers were located above the tibio-tarsal articulation, they probably did not get wet when individuals caught prey. Therefore, they only reflect resting and preening behaviour while floating on the ocean surface. Wilson's Storm-petrels characteristically feed by dipping to pick items from the surface whilst skimming over it or hovering with feet touching the sea surface. Therefore, they are confined to catch prey from the sea surface up to depths shallower than 10–15 cm (Croxall et al. 1988).

Detailed knowledge on prey species during the non-breeding period is lacking as only feather stable isotope analysis are available (Quillfeldt, Thorn, et al. 2017; Quillfeldt et al. 2023; Ausems et al. 2021). Our results could not prove an interspecific significant difference in the feather bulk carbon and nitrogen isotope values but could show a difference in species-specific isotopic niche widths. The broader isotopic niche of Wilson's Storm-petrels may imply greater dietary diversity or variability in resource use, in feeding areas and diet composition, compared to Black-bellied Storm-petrels. Even though the trophic positions (TP_{CSIA}) of the two species did not differ significantly, the narrower isotopic niche of Black-bellied Storm-petrels is reflected in lower intraspecific variations in this species (TP_{CSIA}: 3.6 to 4.0) than in Wilson's Storm-petrels (TP_{CSIA}: 2.8 to 4.1). Ausems et al. (2021) and Quillfeldt, Thorn, et al. (2017) found higher feather $\delta^{13}C$ values in Black-bellied Storm-petrels than in Wilson's Storm-petrels. For feather $\delta^{15}N$ the interspecific difference was not significant (Quillfeldt, Thorn, et al. 2017). In earlier sampling years from the same breeding colony Black-bellied Storm-petrels fed, based on feather stable isotope values, at a higher trophic position than Wilson's Storm-petrels during the non-breeding season, possibly connected to a higher fish intake by Black-bellied Storm-petrels (Quillfeldt, Thorn, et al. 2017; Quillfeldt et al. 2023).

For various reasons, such as a widened foraging range, it is hypothesised that some seabirds feed on myctophids (lanternfish) more during the non-breeding season than during the breeding season. Myctophids may be an important alternative for normally krill-dependent species, such as Wilson's Storm-petrels (Watanuki and Thiebot 2018). Depending on their moulting location, the proportion of myctophid fish in their diet may vary. In our study, the moulting locations of Wilson's Storm-petrels varied in distance from the coast, and myctophid fish are mainly distributed in the oceanic domain and over the shelf slope rather than over the shelf itself and in coastal waters (Nafpaktitis et al. 1977; Watanuki and Thiebot 2018). This possibly is influencing the availability of this prey type, and thus the intake and consequently the Wilson's Storm-petrels' trophic position. At the main non-breeding and moulting sites of the study, myctophids are described as one of the most abundant planktivores and widely distributed (Coté et al. 2019). Leach's Storm-petrels *H. leucorhoa* are known to forage in the same areas around Nova Scotia and Newfoundland for myctophid fish prey (Hedd et al. 2009, 2018). The Newfoundland and Labrador Shelves host a highly productive marine ecosystem and the oceanographic context of this area, with both the cold Labrador Current and warm Gulf Stream, influences the species composition of myctophid fish and crustaceans (Han et al. 2015; Hedd et al. 2018). Increase in sea surface and ocean temperature may affect seabird populations through changes in prey availability (Diamond and Devlin 2003; Han et al. 2015; Hebert et al. 2022; Davoren 2024). General changes over time or annual fluctuations in prey availability may explain the observed variations in results regarding interspecific differences in trophic positions. To be able to interpret these patterns more effectively, further studies on the non-breeding diet composition and general ecology of the storm-petrel species are necessary.

5 | Conclusion

The far-ranging non-breeding distribution of Antarctic storm-petrels emphasizes that both species are likely to face several threats away from their breeding colonies, which may explain decreasing population trends (Ausems et al. 2023). At the time of GLS deployment, all individuals had a well-developed chick, and except for one, all these chicks fledged successfully. Thus, our dataset mostly covers successful breeders. However, the non-breeding behaviour of successful and failed breeders may differ, as has been observed in other seabird species (Bogdanova et al. 2011; Carneiro et al. 2016; Schoombie et al. 2022). This should be checked for both species in future studies. A combination of tracked individuals, covering non-breeders and breeders with different breeding success from different colonies, along with environmental variables, will be necessary to examine the reasons and causes of their apparent inter- and intraspecific non-breeding spatial and trophic segregation.

Author Contributions

Yvonne R. Schumm, Marcela M. Libertelli, Petra Quillfeldt: concept. **Yvonne R. Schumm, Paco Bustamante, Petra Quillfeldt:** methodology. **Yvonne R. Schumm, Mara Centurión, Laura Reyes Jiménez:** investigation. **Yvonne R. Schumm:** formal analysis. **Yvonne R. Schumm:** writing – original draft. **Marcela M. Libertelli, Mara Centurión, Laura Reyes Jiménez, Paco Bustamante, Petra Quillfeldt:** writing – review and editing. **Marcela M. Libertelli, Paco Bustamante, Petra Quillfeldt:** resources. **Marcela M. Libertelli, Petra Quillfeldt:** supervision. **Marcela M. Libertelli, Petra Quillfeldt, Paco Bustamante:** funding.

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Ethics Statement

The study involved wild specimens of Wilson's and Black-bellied Storm-petrels. Animal handling and fieldwork around Carlini

Station was carried out under permits from the Argentine Antarctic Institute, IAA (permit numbers: #2022-FEAMB-CT-GA-79 and #2023-FEAMB-CT-GA-70).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Used R packages and respective version information are given in Supporting Information S2. Stable isotope data is deposited at IsoBank (https://isobank.tacc.utexas.edu/) under dataset record ID 943. Raw data, light intensity and conductivity values, from GLS loggers are stored in PANGAEA Data Publisher (https://doi.org/10.1594/PANGAEA.988099) and processed tracks additionally in the data repository Movebank (www.movebank.org, Movebank ID: 7697526300).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Fitted GAM model for each storm-petrel individuum, with 95% confidence interval (grey shaded), that was used to estimate the timing of an individual storm-petrels moult based upon changes in the daily proportion of time that it spent on the ocean surface, based on saltwater immersion data of geolocators. The purple dashed line represents the cut off for the period where this individual's daily time on the water exceeded 75% of its peak value (cf. Cherel et al. 2016). Bird ID refers to the individual with WSP = Wilson's Storm-petrel and BBSP = Black-bellied Storm-petrel. All birds were tracked in the year 2023. **Figure S2:** Scatter plots depicting the relationships between stable isotope values (δ^{13}C and δ^{15}N) of R6 feathers and based on geolocator data estimated coordinates of the moulting location in Wilson's Storm-petrels *Oceanites oceanicus* ($n = 6$; each black point represents one individual). Blue lines represent linear regression fits with 95% confidence intervals (grey shaded areas). **Figure S3:** Density plots for standard ellipse area (SEA) of the R6-feather isotope data of Black-bellied Storm-petrels *Fregetta tropica* (BBSP) and Wilson's Storm-petrels *Oceanites oceanicus* (WSP). Grey rectangles correspond to credibility intervals (50% inside dark grey boxes, 75% middle grey boxes, 100% outer light grey boxes). Mean standard ellipse area (SEA) is shown by the squares (blue for BBSP, orange for WSP) and overlaid with SEA corrected for sample size (SEAc), depicted by white star symbols. **Figure S4:** Non-breeding distribution of the seven Wilson's Storm-petrels *Oceanites oceanicus* (WSP, orange-tones) with a geolocator. Shown are only the non-breeding sites in the North Atlantic Ocean, for a larger-scale overview see Figure 3. Depicted are (a) the 95% kernel utilisation distribution (KUD, dotted lines) and (b) the 50% KUD (solid line) if individual non-breeding sites in the North Atlantic Ocean. **Figure S5:** Location estimates of adult Wilson's Storm-petrels *Oceanites oceanicus* and Black-bellied Storm-petrels *Fregetta tropica* for time determined as core moult period (Table 2) of flight feathers by individual generalised additive models (GAM) of saltwater immersion data. Individual location estimates (colour coded) are depicted as open circles. The purple square indicates the location of the breeding colony of the tracked birds on King George Island. The pink dashed line represents the equator. **Table S1:** Overview of outermost rectrix (R6) samples used for carbon and nitrogen bulk stable isotope analysis of adult Wilson's Storm-petrels *Oceanites oceanicus* (WSP) and Black-bellied Storm-petrels *Fregetta tropica* (BBSP), sampled near the Argentine Station 'Carlini', King George Island/25 de Mayo Island, South Shetland Islands (62°14′ S, 58°40′ W). Normalised carbon and nitrogen stable isotope values per sample are given with blank correction per mille. **Table S2:** Timing of non-breeding stages for individual birds equipped with geolocators. Dates are given as dd.mm, all within the year of 2023, and represent the start of the respective stage. Species are given as abbreviation within the Bird ID: WSP = Wilson's Storm-petrel *Oceanites oceanicus* and BBSP = Black-bellied Storm-petrel *Fregetta tropica*. If a stage was not present in one individual, this is depicted with '–'. Within Wilson's Storm-petrels the timing is colour-coded with the earliest shaded the lightest and the latest shaded the darkest. **Table S3:** Sizes [km^2] of 50% and 95% kernel utilisation distribution (KUD) of non-breeding sites of individual Wilson's Storm-petrels *Oceanites oceanicus* (WSP) and Black-bellied Storm-petrels *Fregetta tropica* (BBSP). Additionally, longitude (Lon) and latitude (Lat) of the 50% KUD centroid are listed. Location estimates derived from geolocator data. **Table S4:** Proportional overlap [%] of 50% and 95% kernel utilisation distribution (KUD) of non-breeding sites of Wilson's Storm-petrels *Oceanites oceanicus*. Given is the mean from both overlap values, in the bottom part for the 50% KUDs and in the upper part for 95% KUDs. Non-breeding sites were in two oceans: NAO = North Atlantic Ocean, SAO = South Atlantic Ocean. Degree of overlap is coloured graded (darker shades for higher degree of overlap). **Table S5:** Summary of activity data as percentage time spent on water (% 'wet'*) for individual Wilson's Storm-petrels *Oceanites oceanicus* (WSP) and the one tracked Black-bellied Storm-petrel *Fregetta tropica* (BBSP), split for day (sunrise to sunset) and nighttime (sunset to sunrise) and for moon phases (grouped radian value: 0—new, π/2—waxing, π—full and 3π/2—waning moon phase).