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Research

# Reconstructing the historical wintering destinations of seabirds using stable isotope analyses of museum specimens

William F. Mills[1], Juliette Waterman[1], Richard A. Phillips[2], Gayatri Ramakrishnan[1], Ramandeep Nijjar[1], Andrés E. Ibañez[3,4,5], Rona A. R. McGill[6], Lara M. Morales[3,4], Diego Montalti[3,4] and Stuart Black[1]

[1]Department of Geography and Environmental Science, University of Reading, Reading, UK
[2]British Antarctic Survey, Natural Environment Research Council, Cambridge, UK
[3]Sección Ornitología, División Zoología Vertebrados, Museo de la Plata (FCNyM-UNLP), La Plata, Argentina
[4]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina
[5]Departamento de Predadores Tope, Instituto Antártico Argentino (IAA), San Martin, Buenos Aires, Argentina
[6]Stable Isotope Ecology Lab, National Environment Isotope Facility, Scottish Universities Environmental Research Centre, East Kilbride, UK

WFM, 0000-0001-7170-5794; JW, 0009-0009-4326-6099;
RAP, 0000-0002-0208-1444; RARM, 0000-0003-0400-7288;
SB, 0000-0003-1396-4821

Stable isotope analyses of museum specimens provide an opportunity to examine long-term changes in avian migration strategies. Here, we determined stable isotopes of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) in body feathers (reflecting diet during the non-breeding period) sampled from living birds and historical museum specimens to investigate whether brown skuas *Stercorarius antarcticus lonnbergi* from South Georgia and the South Shetland Islands changed their migration strategies during the past 100 years. Feathers sampled from adults in the 2010s at South Georgia had significantly lower $\delta^{13}$C and $\delta^{15}$N values than feathers from the 1910s, potentially indicating a shift from oceanic subtropical and continental shelf-slope waters towards mixed subtropical–subantarctic to subantarctic waters in the Argentine Basin. No isotope values (modern nor historical) from South Georgia were consistent with wintering on the Patagonian Shelf (rather than the shelf-slope). Feathers sampled at the South Shetland

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**Author for correspondence:**
William F. Mills
e-mail: w.f.mills@reading.ac.uk

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Islands in the 2020s had significantly lower $\delta^{13}C$ and $\delta^{15}N$ values than specimens collected 60–100 years previously. A plausible explanation here is reduced reliance on continental shelves and increased use of mixed subtropical–subantarctic to subantarctic waters as wintering destinations over time. Overall, our study highlights how museum collections can be used to investigate changing migration strategies of marine predators, including in remote oceanic ecosystems.

# 1. Introduction

The majority of seabirds show marked changes in their distributions during the different stages of the annual cycle. Outside of the breeding period, seabirds are free from the constraints associated with central-place foraging (e.g. the need to regularly return to the colony to breed, incubate eggs or feed dependent young) and often disperse widely for several consecutive months at sea [1–3]. These seasonal movements can occur over vast geographic scales (100s–1000s km), with some individuals migrating to entirely different ecosystems [1]; indeed, seabirds undertake some of the longest known migrations in the animal kingdom, including from pole to pole in the case of the Arctic tern *Sterna paradisaea* [4]. As a result, most research has focused on the ecology of seabirds during the breeding period (when individuals are accessible for sampling) compared with the non-breeding period. Different seabird species from the same breeding site can show contrasting migration strategies [1,2], and there is often extensive intraspecific variation related to intrinsic factors such as sex, age, breeding status and individual preference [1,3,5–8]. For example, due to their greater overall wing area and loading, male wandering albatrosses *Diomedea exulans* from the remote subantarctic islands of South Georgia are able to exploit stronger winds at higher latitudes than females during the non-breeding period, including in the Drake Passage and Humboldt Current [7]. However, the migration strategies of seabirds can shift over time and in response to natural and anthropogenic environmental changes; for instance, the wintering areas of thin-billed prions *Pachyptila belcheri* from the Falkland Islands have shifted polewards since the early twentieth century, probably due to increasing sea temperatures in the region [9]. Variation in the diets and at-sea distributions of seabirds can have important repercussions for their exposure to anthropogenic threats, such as the likelihood of incidental mortality (by-catch) in commercial fisheries and exposure to pollutants [10,11], and may lead to carry-over effects on performance in the subsequent breeding season [11,12]. Understanding the threats posed to seabirds during all stages of the annual cycle is especially important given their generally poor conservation status relative to other vertebrate groups [13,14].

Stable isotope analysis of feathers sampled from adult seabirds at the breeding colony provides a method of inferring diets and distributions during the preceding non-breeding period [1–3,5]. This approach relies on the fact that the isotopic composition of seabird feathers reflects that of their prey during tissue formation and that moult generally takes place during the non-breeding period, since both breeding and feather replacement are energetically expensive [15–17]. Stable isotope ratios of carbon ($^{13}C:^{12}C$, expressed as $\delta^{13}C$ values in per mil units, ‰) and nitrogen ($^{15}N:^{14}N$, $\delta^{15}N$) are the most frequently determined in avian tissues and provide information on the bionomic (resources) and scenopoetic (habitat) components of the ecological niche, respectively [17,18]. Typically, $\delta^{13}C$ values are used to infer the feeding areas (carbon sources) of seabirds, such as the use of inshore versus offshore, benthic versus pelagic habitats, or the use of different latitudes or water masses [1–3,19]. The utility of $\delta^{15}N$ values relies on the stepwise increase with trophic level [20]; however, baseline $\delta^{15}N$ values can also vary spatially in marine environments [17]. In the southwest Atlantic Ocean sector of the Southern Ocean, baseline $\delta^{13}C$ values (as represented by particulate organic matter) show a broad decline with latitude, from the subtropics towards the Antarctic continent, and the highly productive waters of the Patagonian Shelf are characterized by elevated $\delta^{13}C$ and $\delta^{15}N$ values [9,21]. These broad-scale spatial gradients in baseline stable isotope values ('isoscapes') are reflected in the tissues of migratory seabirds feeding in the region [1,5,9,22]. White-chinned petrels *Procellaria aequinoctialis* that breed at South Georgia, for instance, which are known from tracking data to migrate to the Patagonian Shelf and shelf-break waters [23,24], have correspondingly high body feather $\delta^{13}C$ and $\delta^{15}N$ values, reflecting their diet during that part of the annual cycle [1]. Since keratin is metabolically inert, the isotopic signature of diet at the time of feather growth is preserved indefinitely [17]. Hence, one application of the stable isotope approach is to analyse feathers from museum specimens and more recent samples to undertake retrospective studies of possible changes in migration patterns over decadal to centennial time scales, depending on the availability of historical samples [25,26].

Using stable isotopes, our study investigated the migration (non-breeding or wintering) patterns of brown skuas *Stercorarius antarcticus lonnbergi* from two breeding locations in the Southern Ocean: South Georgia (subantarctic) and the South Shetland Islands (Antarctic). The main objective of our study was to investigate if migration patterns of birds from these populations have changed during the past 100 years by determining $\delta^{13}$C and $\delta^{15}$N values in feathers of contemporary birds and museum skins. A secondary objective was to test for sexual segregation. Brown skuas have a circumpolar breeding distribution in the Southern Hemisphere, including on subantarctic islands and at higher latitudes, such as the Antarctic Peninsula [27]. While breeding, brown skuas are opportunistic predators and scavengers. At South Georgia, incubating brown skuas feed on placentae and carrion of Antarctic fur seals, *Arctocephalus gazella* and to some degree on burrowing petrels and other seabirds [28], whereas at the South Shetland Islands, penguin eggs and chicks (*Pygoscelis* spp.) are the most important prey [29]. However, during the non-breeding period, brown skuas have largely pelagic distributions, and unlike the congeneric south polar skua *S. maccormicki*, which is a transequatorial migrant [30], all brown skuas tracked with geolocators remained within the Southern Hemisphere [16,30–34]. Previous tracking and stable isotope studies demonstrate the contrasting migration strategies of brown skuas from different populations [5,15,31–35]. For instance, the individuals from South Georgia that were tracked with geolocators in the winters of 2002 and 2012 predominantly targeted deep (approx. 5000 m), oceanic waters in the Argentine Basin and elsewhere between the Antarctic Polar Front (APF) and the northern extent of the subtropical front (STF) [15,31]. In contrast, individuals from the South Shetland Islands (tracked in 2007–2010) migrated to the Patagonian Shelf, Argentine Basin and the southern Brazil Shelf (to a lesser degree) [32]. It is unclear whether migration strategies have always differed between these populations or diverged only in recent decades. Our study takes place within the context of important historical changes to pelagic marine ecosystems in the southwest Atlantic sector of the Southern Ocean during the twentieth century, with potentially major implications for seabird diets and distributions, including the onset of commercial fisheries, large-scale removal of marine megafauna (e.g. baleen whales and pinnipeds) and climate change-related alterations to marine food webs [36,37].

# 2. Material and methods

## 2.1. Study sites and feather sampling

Feather sampling of contemporary brown skua populations was undertaken at the Potter Peninsula, King George Island/Isla 25 de Mayo, South Shetland Islands (62°15′ S, 58°40′ W), and at Bird Island, South Georgia (54°00′ S, 38°03′ W), in January 2024 and December 2014, respectively. King George Island is the largest of the South Shetland Islands and is located approximately 130 km to the northwest of the Antarctic Peninsula, whereas Bird Island is situated in the northwest of the South Georgia archipelago, which is approximately 300 km south of the APF on the Scotia Arc (figure 1). Adult birds were captured during the incubation period with a noose, hand net or by hand on the nest. A random selection of fully grown body feathers was pulled individually from the breast at the Potter Peninsula and from the lower back at Bird Island. Feathers were subsequently stored in sealed envelopes or plastic bags at an ambient temperature before laboratory analyses. Although a small minority of body feathers may be regrown by skuas during the breeding period [35], the vast majority are moulted during the non-breeding period [15,16], and hence the stable isotope values of fully grown body feathers that were sampled in our study are highly likely to reflect the diets and distributions of brown skuas during the non-breeding period before sampling [5]. All birds from these populations were sexed through the analysis of DNA extracted from blood samples [41]. In addition, body feathers were sampled from the breast of museum specimens of brown skuas using stainless-steel tweezers, with sampling restricted to specimens with known collection locations and dates that corresponded to the breeding period. Feathers were sampled from historical museum specimens of brown skuas at The Natural History Museum (Tring, UK), National Museum of Natural History, Smithsonian Institution (Washington, DC, USA), American Museum of Natural History (New York, USA), La Plata Museum (La Plata, Argentina), Museum Stavanger (Stavanger, Norway), Natural History Museum at the University of Oslo (Oslo, Norway), University Museum of Bergen (Bergen, Norway) and the Academy of Natural Sciences of Drexel University (Philadelphia, USA). The majority of museum specimens had a sex recorded in the accession information (electronic supplementary material, table

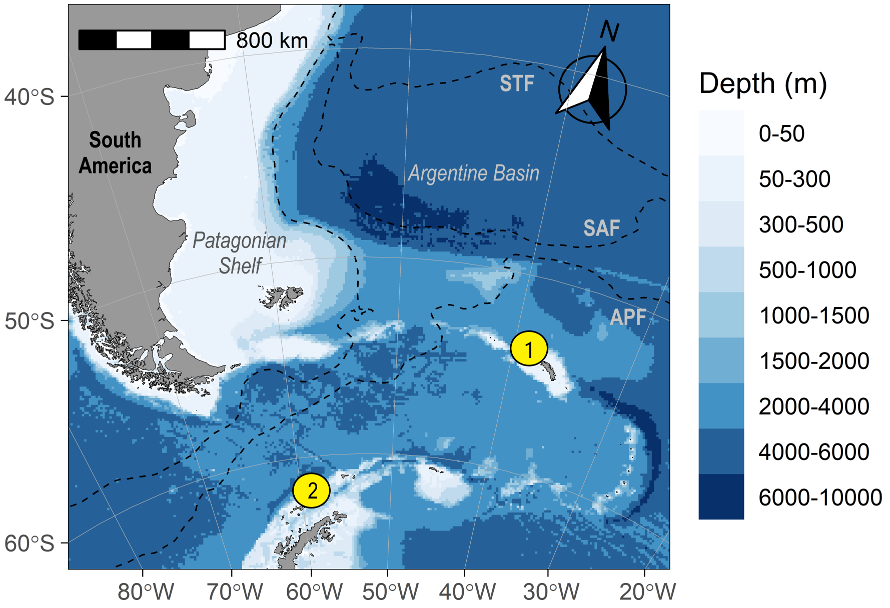

**Figure 1.** Locations of the brown skua *Stercorarius antarcticus lonnbergi* study sites in the southwest Atlantic Ocean sector of the Southern Ocean: (1) Bird Island, South Georgia; and (2) King George/25 de Mayo Island, South Shetland Islands. The map shows these sites in relation to approximate positions of the APF, subantarctic front and STF according to the 'Park/Durand' fronts from the orsifronts package in R. This map was created using the ggOceanMaps package in R [38–40].

S1). All data generated in our study are included alongside associated museum accession numbers in electronic supplementary material, table S1.

## 2.2. Stable isotope analysis

External contamination was removed from brown skua feathers using successive rinses of chloroform : methanol solution (2 : 1 v/v) and ultra-pure water (Milli-Q®). Cleaned feathers were then dried in an oven (40°C for 48 h). Following a previous stable isotope study of brown skuas [5], multiple feathers were pooled per individual and homogenized with sterilized stainless-steel scissors. Subsamples (approx. 0.2 mg) of homogenized feathers were weighed into tin capsules (6 × 4 mm) on a Sartorius Cubis™ microbalance. Stable isotope analyses of bulk feather samples were carried out at the Chemical Analysis Facility of the University of Reading through a continuous flow-isotope ratio mass spectrometer coupled to a ThermoFisher™ DeltaV Advantage fitted with an Isolink CNSOH Temperature Conversion Elemental Analyzer (TC/EA) and smart function. Results are reported in the conventional $\delta$ notation in per mil (‰) units relative to the international standards Vienna PeeDee Belemnite (VPDB) and atmospheric $N_2$ (AIR) for carbon and nitrogen, respectively. Data were drift and stretch corrected using in-house (MethR ($\delta^{13}C = -27.5$ ‰; $\delta^{15}N = -4.1$ ‰), Reading Porcine Gelatin ($\delta^{13}C = -21.5$ ‰; $\delta^{15}N = +5.0$ ‰) and Reading Fish Skin ($\delta^{13}C = -15.6$ ‰; $\delta^{15}N = +14.0$ ‰)) and international standards (USGS61 ($\delta^{13}C = -35.05$ ‰; $\delta^{15}N = -2.87$ ‰), USGS62 ($\delta^{13}C = -14.79$ ‰; $\delta^{15}N = +20.17$ ‰) and USGS63 ($\delta^{13}C = -1.17$ ‰; $\delta^{15}N = +37.83$ ‰)). All samples were analysed in triplicate, and mean values were used in statistics and figures. Measurement errors were ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values.

## 2.3. Data analysis

All data analysis for this study was carried out in R version 4.2.1 [42]. Data were visualized with the ggplot2 package in R [43]. Increasing emissions of anthropogenic carbon dioxide ($CO_2$) since the beginning of the Industrial Revolution, which is depleted in $^{13}C$, have resulted in declining baseline $\delta^{13}C$ values in natural systems (termed the 'Suess effect') [44,45]. Hence, raw $\delta^{13}C$ values of historical feathers sampled from museum skins in this study were normalized to the final year of the dataset ('analysis year') using a year-dependent correction factor following Quillfeldt *et al.* [9] and Hilton *et al.* [45] (correction factor = $-1 + 1.1^{(\text{final year} - \text{sample collection year}) \times 0.027}$). The Suess-corrected $\delta^{13}C$ values were used in data visualization and subsequent statistical analyses. Feather $\delta^{13}C$ and $\delta^{15}N$ values

**Table 1.** Stable isotope values (‰) of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) determined in body feathers of adult brown skuas *Stercorarius antarcticus lonnbergi* sampled from two breeding sites in the southwest Atlantic sector of the Southern Ocean: Bird Island, South Georgia and King George/25 de Mayo Island, South Shetland Islands. Data are means (±s.d.) with ranges in parentheses. Feather $\delta^{13}$C values of museum skins (see main text) were corrected for the Suess effect following Quillfeldt *et al.* [9].

| breeding site | decade | *n* | $\delta^{13}$C (‰, VPDB) | $\delta^{15}$N (‰, AIR) |
|---|---|---|---|---|
| South Georgia | 1900s | 1 | −18.5 | 11.1 |
| | 1910s | 15 | −17.0 ± 0.7 (−18.3 to −16.1) | 12.2 ± 1.4 (9.9–15.1) |
| | 1970s | 2 | −16.3 ± 0.4 (−16.5 to −16.0) | 11.5 ± 0.1 (11.5–11.5) |
| | 2010s | 26 | −18.5 ± 0.7 (−20.1 to −17.2) | 11.1 ± 1.1 (9.1–13.1) |
| South Shetland Islands | 1920s | 10 | −15.4 ± 1.1 (−17.5 to −14.0) | 17.1 ± 2.5 (12.6–19.5) |
| | 1940s | 8 | −16.1 ± 0.9 (−17.6 to −14.6) | 15.2 ± 2.6 (12.2–20.7) |
| | 1960s | 7 | −15.4 ± 1.7 (−18.7 to −14.1) | 16.3 ± 3.8 (10.3–19.7) |
| | 2020s | 28 | −18.0 ± 1.3 (−20.2 to −15.1) | 14.0 ± 2.2 (10.7–19.6) |

(analysed separately for the two breeding sites) were first assessed for the assumptions of normality and homogeneity of variances using Shapiro–Wilk and Levene's tests, respectively. At South Georgia, differences in $\delta^{13}$C and $\delta^{15}$N values between decades and sexes were assessed using *t*-tests or Wilcoxon tests. Data from 1900 to 1909 and 1970 to 1979 at South Georgia were included in figures but omitted from analyses due to small sample sizes (table 1). At King George Island, Kruskal–Wallis tests and subsequent *post hoc* Dunn's tests were used to assess differences in $\delta^{13}$C and $\delta^{15}$N values among decades. Analyses of sex differences at King George Island were restricted to the 2020s due to the low number of sexed birds in other decades and were investigated using *t*-tests or Wilcoxon tests. Decadal and sex differences were investigated separately in all cases, as not all birds were of known sex. The threshold for statistical significance was set at $\alpha = 0.05$.

To enhance interpretation of the data, feather $\delta^{13}$C and $\delta^{15}$N values determined in this study were visualized in relation to those of fully grown body feathers of adult white-chinned petrels and brown skuas from South Georgia, which reflect diet during the non-breeding period when their distributions are well-characterized [1,15]. Stable isotope values of growing body feathers of brown skuas at King George Island are also shown [35]. These data provide isotopic signatures for: (i) Patagonian Shelf and shelf-break waters; (ii) mixed subtropical–subantarctic to subantarctic waters within the Argentine Basin (37–52°S), and elsewhere between the APF and the STF; and (iii) high-latitude Antarctic waters around the South Shetland Islands. Isotopic signatures reflecting the approximate positions of biogeographic boundary zones (e.g. Antarctic (south of the APF), subantarctic (between the APF and subantarctic front), subtropical waters and continental shelf, derived from tracked seabirds from South Georgia with contrasting distributions, are also presented [1].

## 3. Results

Body feather $\delta^{13}$C and $\delta^{15}$N values were determined for 26 and 28 individuals from contemporary populations, and 18 and 25 historical museum specimens of brown skuas that were collected from South Georgia and King George Island, respectively (table 1). At both locations (figure 2, electronic supplementary material, figure S1), all feathers exhibited higher $\delta^{13}$C values than the mean $\delta^{13}$C values of growing body feathers of brown skuas at King George Island [35]. At South Georgia, $\delta^{13}$C and $\delta^{15}$N values of feathers sampled in the 2010s were significantly lower than those of museum specimens collected during the 1910s (*t*-tests, $t = -6.47$, $p < 0.01$ and $t = -2.69$, $p < 0.05$, respectively) (figures 2 and 3). There were no significant differences between feather $\delta^{13}$C and $\delta^{15}$N values of males and females sampled at South Georgia in the 2010s ($t = -1.67$, $p = 0.11$ and $t = -1.25$, $p = 0.22$, respectively) (electronic supplementary material, figure S2). However, in the 1910s, feather $\delta^{15}$N values of males were significantly higher than females at South Georgia ($t = 3.48$, $p < 0.01$), but $\delta^{13}$C values were similar (Wilcoxon test, W = 16, $p = 0.22$) (electronic supplementary material, figure S2). At King George Island, feather $\delta^{13}$C and $\delta^{15}$N values differed significantly among decades (Kruskal–Wallis tests, $\chi^2 = 27.3$, $p < 0.001$ and $\chi^2 = 8.4$, $p < 0.05$, respectively) (figures 2 and 3). *Post hoc* Dunn's tests indicated that feather $\delta^{13}$C values were significantly lower in the 2020s than in other decades, among which there were no

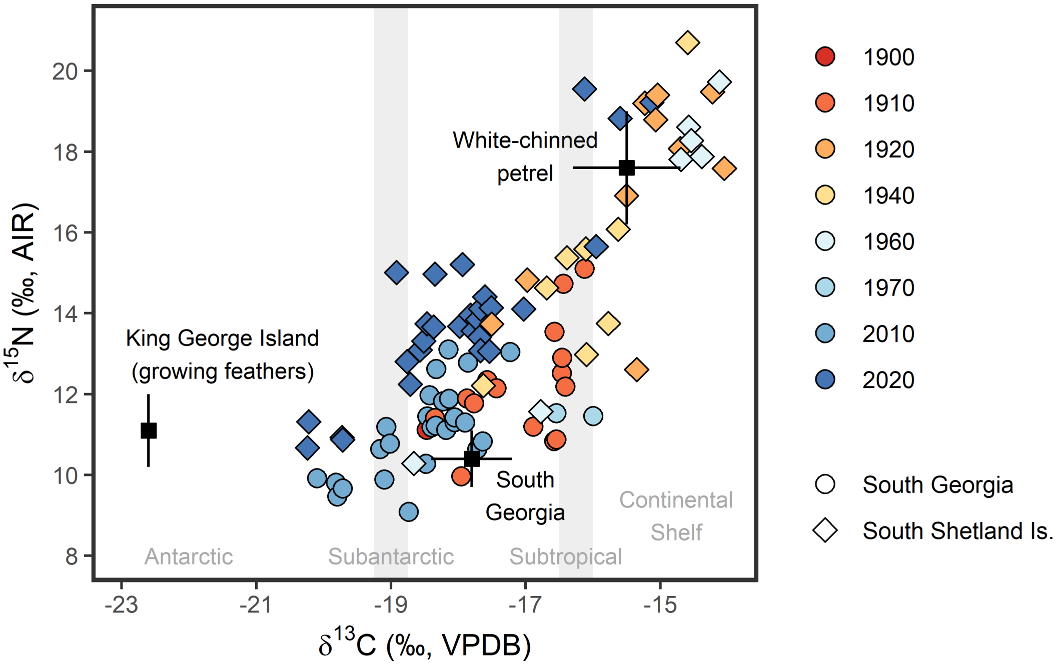

**Figure 2.** Stable isotope values (‰) of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) measured in body feathers of adult brown skuas *Stercorarius antarcticus lonnbergi* from South Georgia and South Shetland Islands. Black squares and error bars are mean (±s.d.) $\delta^{13}$C and $\delta^{15}$N values of fully grown body feathers of white-chinned petrels *Procellaria aequinoctialis* ($n = 16$) and brown skuas ($n = 40$) from Bird Island, South Georgia (sampled in 2001/2002) [1,15], and growing body feathers of brown skuas from King George/25 de Mayo Island (South Shetland Islands, sampled in 2011/2012, $n = 3$) [35]. Note that the $\delta^{13}$C error bars of the latter fall within the width of the point. Grey vertical lines and text represent the approximate isotopic signatures of biogeographic boundary zones (Antarctic, subantarctic, subtropical waters, continental shelf) derived from tracked migratory seabirds in the southwest Atlantic sector of the Southern Ocean [1]. Feather $\delta^{13}$C values of museum specimens (see main text) were corrected for the Suess effect [9].

significant differences (figures 2 and 3). Feather $\delta^{15}$N values were significantly lower in the 2020s than the 1920s, whereas $\delta^{15}$N values from the 1940s and 1960s were not significantly different from other decades (figure 3). There were no significant sex differences in feather $\delta^{13}$C and $\delta^{15}$N values of brown skuas at King George Island in the 2020s ($t = 0.64$, $p = 0.53$ and $t = 0.23$, $p = 0.82$, respectively) (electronic supplementary material, figure S2).

# 4. Discussion

Comparisons between stable isotope values of archived tissues (e.g. from historical museum collections or bones recovered from archaeological contexts) and contemporary samples provide opportunities to investigate long-term changes in the diets and distributions of birds [25,26], and to infer the consequences of past and ongoing environmental change [46]. In this study, we determined stable isotope values of body feathers of brown skuas from contemporary populations and historical museum specimens that were collected from two breeding sites in the southwest Atlantic sector of the Southern Ocean (South Georgia and King George Island). The objective was to investigate whether the migration strategies of these populations have changed over the past 100 years in a region that has been profoundly impacted by anthropogenic activities during the twentieth century, including major modifications to food webs caused by the onset of commercial fisheries and climate change [36,37]. Feather $\delta^{13}$C values of all individuals were higher (i.e. less negative) than the mean $\delta^{13}$C values of growing body feathers of brown skuas at King George Island [35], confirming that no birds in this study used high latitude waters around the Antarctic Peninsula during their non-breeding periods, and that no feathers sampled from King George Island were grown while at the breeding site (figure 2).

The stable isotope values of feathers collected from brown skuas at South Georgia in the 2010s were similar to those of tracked birds sampled at the same site in the early 2000s (see figure 3 in Phillips *et al.* [15]); hence, as discussed by Mills *et al.* [5], it is likely that these birds also used oceanic, mixed

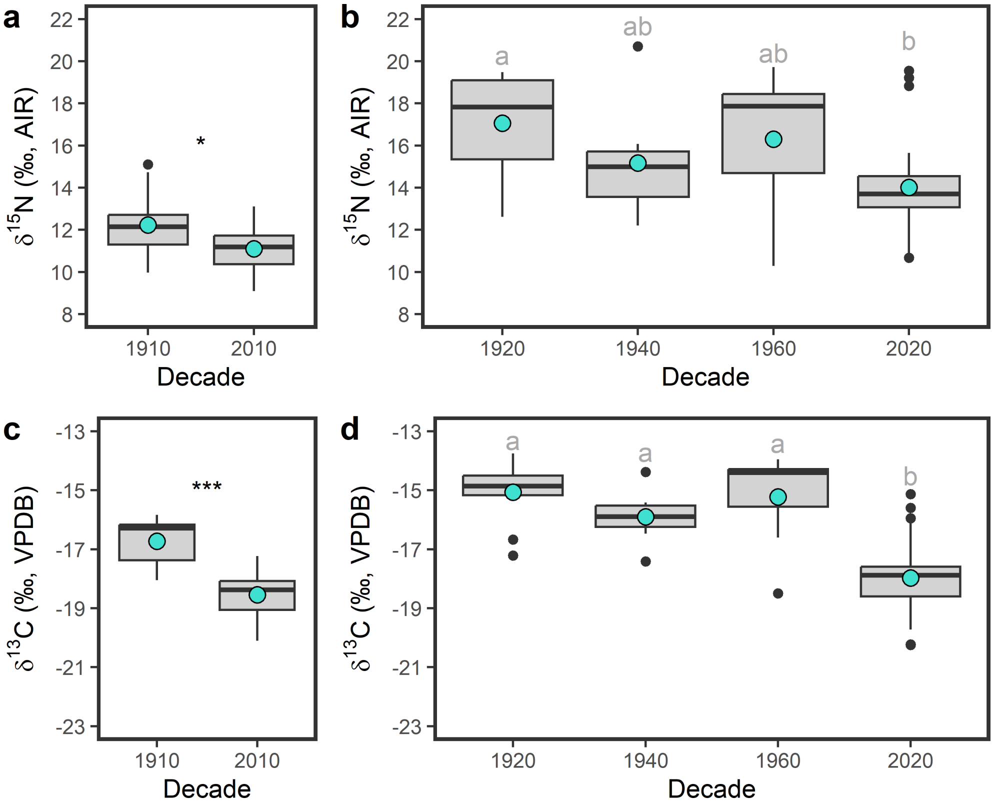

**Figure 3.** Boxplots showing decadal changes in stable isotope values (‰) of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) of body feathers of brown skuas *Stercorarius antarcticus lonnbergi* sampled from Bird Island, South Georgia (a, c), and King George/25 de Mayo Island, South Shetland Islands (b, d). Boxplots show medians (horizontal lines), interquartile range (IQR; boxes), the lowest and highest values within 1.5 × IQR (whiskers) and outliers (black points). Filled blue circles are mean values. Boxes sharing the same letters were not significantly different according to *post hoc* Dunn's tests. Where releveant, statistical significance is indicated above boxes ($* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$). Feather $\delta^{13}$C values of museum skins (see main text) were corrected for the Suess effect [9].

subtropical–subantarctic to subantarctic waters in the non-breeding period, predominantly within the Argentine Basin [15,31] (figure 1). These waters are not especially productive during winter (as inferred from chlorophyll-*a* concentrations), particularly when compared with those on the Patagonian Shelf; nonetheless, no feathers from South Georgia (modern nor historical) had isotopic signatures that were similar to those of white-chinned petrels from the same site, implying that the waters on the Patagonian Shelf have not been important wintering areas for this population over the past 100 years (figure 2). Although there are few conventional diet data available during the non-breeding period, brown skuas from South Georgia are thought to have mixed diets while wintering in the Argentine Basin, probably comprising zooplankton and low-trophic-level cephalopods and fish [15,31]. The reason why this population should target the deep waters of the Argentine Basin remains elusive, but could be related to the avoidance of competition with the abundant scavengers that are much larger or better divers, which winter on the Patagonian Shelf (e.g. many albatrosses and medium–large petrels), as well as skuas from other populations in the region.

Historical museum feathers collected in the 1910s at South Georgia had significantly higher $\delta^{13}$C and $\delta^{15}$N values than those of birds sampled in the 2010s (figures 2 and 3). High $\delta^{13}$C and $\delta^{15}$N values of adult feathers typically indicate use of more northerly waters and continental shelves by migratory seabirds in our study region [1,4]. There are two potential explanations for these results. First, these significant differences may indicate long-term changes in the wintering areas of this population during the past 100 years. However, there was a degree of overlap among feather isotope values from the 1910s and 2010s, with a subset of historical feathers having similar values to those of modern birds (e.g. 39% of $\delta^{13}$C values of historical feathers were within the range of samples from the 2010s), and so presumably used similar water masses (figure 2). The differences in mean values were driven by a subset of birds with $\delta^{13}\mathrm{C} \geq -17.5$ ‰, which are isotopic signatures indicative of either an oceanic subtropical signature or the use of shelf-break waters (figure 2), potentially around the Falkland Escarpment or towards the Brazil–Falklands confluence and the southern Brazil Shelf (figure 1). Hence, the overall distribution of brown skuas from South Georgia may have shifted away from these wintering areas during the twentieth century, and towards mixed subtropical–subantarctic to subantarctic waters. Although we cannot be definitive about the drivers of these potential changes in distributions, Quillfeldt *et al.* interpreted declining feather $\delta^{13}$C values of thin-billed prions from the Falkland Islands (1913–2005) as a polewards shift in distribution, which was driven by increasing regional sea temperatures and corresponding bottom-up changes in marine food webs [9]. Indeed, there have been important changes in the distribution of lower trophic-level organisms within the South Atlantic Ocean over the last century; for instance, the distribution of Antarctic krill *Euphausia superba* has contracted polewards over the past 90 years, with reduced densities towards the northern extent of its range [47,48]. Hence, it is plausible that any changes in brown skua distributions over time could also be driven by bottom-up effects of warming temperatures (e.g. changes in the abundance and occurrence of key prey). The changes observed here are not as pronounced as those of thin-billed prions [9], potentially because brown skuas are generalist feeders and so less reliant on tracking the distribution of specific prey. Alternative factors, such as changes in the levels of competition, may also play a role in these shifting distributions.

Baseline $\delta^{13}$C values are closely associated with phytoplankton growth (i.e. primary production), and so reduced primary production within the feeding areas of brown skuas over the past 100 years may lead to lower baseline $\delta^{13}$C values [43]. Our study was unable to test this hypothesis directly, given that low-trophic-level marine organisms (e.g. zooplankton) and water samples are rarely available in historical collections, especially from remote oceanic regions such as our study area, and because brown skuas feed over wide geographic areas during the non-breeding period. As such, it is challenging to select relevant indicators of isotopic baseline changes. However, a stable isotope study of cephalopod beaks regurgitated by wandering albatrosses at South Georgia found no consistent temporal trends in $\delta^{13}$C values among Antarctic, subantarctic and subtropical cephalopod species in the southwest Atlantic Ocean from the mid-1970s to mid-2010s [49]. Moreover, as stated above, there was a substantial overlap in $\delta^{13}$C values between historical and modern feathers, and the single feather from the 1900s had a $\delta^{13}$C value that was comparable to that of feathers collected in the 2010s. Hence, there is some evidence to suggest that baseline changes are not necessarily the most important factor contributing to the differences observed here.

Feather stable isotope values of brown skuas from King George Island had a different statistical distribution to those of birds from South Georgia (figure 2). However, these data were similarly distributed to those of brown skuas breeding at the South Orkney Islands and the Antarctic Peninsula [5], and to a previous study of brown skuas on King George Island in the early 2010s [35]. The majority of feathers collected from King George Island in the 2020s showed similar $\delta^{13}$C values to those collected from South Georgia in the 2010s, indicating that they also used mixed subtropical–subantarctic to subantarctic waters (figure 2). However, these feathers generally showed higher $\delta^{15}$N values, suggesting that birds from King George Island may consume a greater proportion of higher trophic-level prey (or a lesser amount of zooplankton) within this wintering area. Other feathers had stable isotope values that were consistent with feeding on continental shelves or shelf-break waters (i.e. very similar to those of tracked white-chinned petrels from South Georgia). This suggests that, unlike the vast majority of brown skuas from South Georgia, some birds from King George Island may spend the winter on, or near, the Patagonian Shelf [5], corroborating previous tracking data [32]. Although relatively few skuas are observed on the Patagonian Shelf during winter, those individuals that are present probably include brown skuas originating from Antarctic breeding locations (e.g. Antarctic Peninsula, South Orkney Islands and the South Shetlands) and Falkland skuas *S. antarcticus antarcticus*, which mainly wintered in subantarctic waters around the central Patagonian shelf break, and to a lesser degree on the open shelf, in the mid-2000s [15]. Feathers sampled in the 2020s at King George Island had significantly lower $\delta^{13}$C values than those of museum specimens collected in the 1920s, 1940s or 1960s (figures 2 and 3). Moreover, $\delta^{15}$N values were significantly lower in the 2020s than in the 1920s, whereas those from the 1940s and 1960s were not significantly different from other decades. These results appeared to be driven by a lower proportion of modern feathers having isotopic signatures corresponding to feeding on the continental shelf (i.e. higher $\delta^{13}$C and very high $\delta^{15}$N values) in comparison with historical feathers (figures 2 and 3). This is despite the larger sample size of the former. Given that the Patagonian Shelf remains highly productive, a reduced reliance on continental shelf waters as a wintering area could reflect the greatly increased pressure from expanding fisheries over time, which is a major threat to marine ecosystems globally and a key driver of seabird population declines [13,14], and may have altered the structure and dynamics of food webs on the Patagonian Shelf. Moreover, skuas are probably outcompeted by albatrosses and medium–large petrels behind vessels, which dominate there on the Patagonian Shelf. Such hypotheses require further investigation. A reduction in primary productivity and baseline $\delta^{13}$C values is unlikely to apply to the birds from King George Island, as within each decade, the data are essentially bimodal in distribution (i.e. corresponding to either a continental shelf or mixed subtropical–subantarctic to subantarctic waters signature) and hence the decadal changes are unlikely to be driven by a gradual change in isotopic baselines.

Finally, there were no significant differences in feather $\delta^{13}$C and $\delta^{15}$N values of males and females sampled at South Georgia in the 2010s [5], nor at King George Island in the 2020s. Indeed, although brown skuas show sexual size dimorphism, such that females are larger than males [50], studies at South Georgia and King George Island found no sex differences in the distribution of tracked birds [15,31,33]. However, in the 1910s at South Georgia, feather $\delta^{15}$N values of males were significantly higher than females, but $\delta^{13}$C values were similar. This might suggest that males in the 1910s were feeding at slightly higher trophic levels than females at this time, but that their overall distributions were similar. One hypothesis as to why the trophic niches of males and females have become more similar over time is that the availability and spatial distribution of resources is more homogeneous within their contemporary compared with historical non-breeding areas, reducing the scope for sexual segregation. Overall, this study highlights that avian museum collections are critical resources for retrospective ecological research, and our study illustrates how stable isotope analyses can be used to undertake historical studies (over centennial time scales) of seabird migration strategies, including in remote marine ecosystems such as in the Antarctic and subantarctic.

**Ethics.** Handling and feather sampling of brown skuas at Bird Island in the 2010s was approved by the British Antarctic Survey Animal Welfare and Ethics Review Body and was carried out under permits from the Government of South Georgia and the South Sandwich Islands. Feather sampling of birds at the Potter Peninsula in 2024 followed relevant international, national and institutional guidelines related to the sampling, care and experimental use of animals, as established by Article III, Annex II of the Madrid Protocol, Law 24.216 (Taking, Harmful Intrusion and Introduction of Species), within the framework of the projects evaluated and approved by the Environment Office of the Instituto Antártico Argentino and the Dirección Nacional del Antártico (permit number: 2023-FEAMB-CT-GA-26). All protocols were evaluated and approved by the Institutional Committee for the Care and Use of Study Animals (CICUAE) of Natural Science and Museum Faculty (FCNyM-UNLP). Animal manipulation time did not exceed 8 minutes to avoid handling stress responses.

**Data accessibility.** The original data are included in the article and electronic supplementary material [51]. Further inquiries can be directed to the corresponding author.

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** W.F.M.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft; J.W.: investigation, methodology, writing—review and editing; R.A.P.: resources, writing—review and editing; G.R.: investigation, writing—review and editing; R.N.: investigation, writing—review and editing; A.E.I.: resources, writing—review and editing; R.A.R.M.: investigation, writing—review and editing; L.M.M.: resources, writing—review and editing; D.M.: resources, writing—review and editing; S.B.: methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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