



# Migration strategies of skuas in the southwest Atlantic Ocean revealed by stable isotopes

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## Abstract

Stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) were measured in feathers to compare the non-breeding distributions and habitat use of adult brown skuas *Stercorarius antarcticus lönnerbergi* from high-latitude colonies at Esperanza/ Hope Bay (Antarctic Peninsula, 63°S) and Signy Island (South Orkneys, 60°S), with those from Bird Island (South Georgia, 54°S), which have also been tracked previously using geolocators. Breeding colony, but not sex, had a significant effect on feather  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Feather stable isotope data from South Georgia birds mostly corresponded to oceanic, mixed subtropical–subantarctic to subantarctic waters, which agrees with the tracking data, as did a subset of the birds from the two higher latitude populations. However, other individuals displayed feather stable isotope ratios that were consistent with continental shelf or shelf-slope waters, suggesting that unlike the vast majority of brown skuas from South Georgia, many birds from higher latitude colonies spend the non-breeding season on, or near, the Patagonian Shelf. These population-level differences may have implications for exposure to anthropogenic threats or have carryover effects on subsequent breeding behaviour or performance.

**Keywords** Seabirds · Carbon-13 · Nitrogen-15 · Antarctica · Southern Ocean

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## Introduction

Brown skuas *Stercorarius antarcticus lönnerbergi* have a circumpolar breeding distribution in the Southern Hemisphere, including on subantarctic islands and at higher latitudes (Ritz et al. 2008). During the breeding period, brown skuas are opportunistic predators and scavengers, with differences in diet composition among colonies reflecting the seasonal availability of locally abundant prey (Burton 1968; Reinhardt et al. 2000; Phillips et al. 2004; Anderson et al. 2009; Graña Grilli and Montalti 2015; Borghello et al. 2019; Ibañez et al. 2022; Mills et al. 2022). For instance, during incubation, brown skuas at South Georgia predominantly make coastal foraging trips and feed on the placenta and carrion of Antarctic fur seals *Arctocephalus gazella* and to some degree on burrowing petrels (Phillips et al. 2004; Anderson et al. 2009; Carneiro et al. 2014). Brown skuas breeding at more southerly colonies also feed mainly on land but on penguin eggs and chicks, and shift later in the season to consume marine resources (i.e., fish and cephalopods) (Carneiro et al. 2015; Ibañez et al. 2022).

During the non-breeding period, brown skuas are no longer restricted by the central-place foraging constraint and can disperse widely. Brown skuas from South Georgia, King George/25 de Mayo Island (South Shetland Islands), Chatham, Crozet and Kerguelen Islands have all been tracked during the non-breeding period (Phillips et al. 2007; Carneiro et al. 2016a; Krietsch et al. 2017; Delord et al. 2018; Schultz et al. 2018). Unlike the closely-related south polar skua *S. maccormicki*, which can undertake trans-equatorial migrations (Kopp et al. 2011), brown skuas breeding in the southwest Atlantic Ocean sector of the Southern Ocean remain within the Southern Hemisphere during the non-breeding period. Birds from South Georgia tracked in the 2002 and 2012 winters targeted deep, oceanic waters, mostly within the Argentine Basin, or elsewhere between the Antarctic Polar Front (APF) and the northern extent of the subtropical front (STF) (Phillips et al. 2007, 2009; Carneiro et al. 2016a). In contrast, those from King George Island tracked from 2007 to 2010 spent the non-breeding season over the Patagonian Shelf, Argentine Basin and, to a lesser extent, the southern Brazil Shelf (Krietsch et al. 2017). Brown skua populations on the Antarctic Peninsula and South Orkney Islands have not been tracked; hence, their migration strategies and wintering areas are currently unknown.

Stable isotope ratios of feathers are routinely used to investigate the foraging ecology of adult seabirds during the non-breeding period, which is when moult generally takes place (Cherel et al. 2000; Phillips et al. 2009; Mills et al. 2021). Feather stable isotope ratios reflect those of prey during tissue formation, and because keratin is metabolically inert, the dietary signal is preserved indefinitely. Stable isotope ratios of carbon ( $^{13}\text{C}$ : $^{12}\text{C}$ , expressed as  $\delta^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ : $^{14}\text{N}$ ,  $\delta^{15}\text{N}$ ) are most commonly measured in seabird tissues. The utility of  $\delta^{15}\text{N}$  values relies on a stepwise increase at each trophic level ( $-3$ – $5$  ‰), whereas  $\delta^{13}\text{C}$  values can provide spatial information on feeding areas (Hobson and Clark 1992; Bearhop et al. 2002; Cherel and Hobson 2007; Jaeger et al. 2010). This includes a dependence on an inshore vs. offshore, benthic vs. pelagic diet, and latitude/water mass where gradients exist, as is the case in the Southern Ocean (Cherel and Hobson 2007; Phillips et al. 2009; Jaeger et al. 2010). In this study, by measuring stable isotope ratios in feathers, we investigated the migration strategies and habitat use of brown skuas during the non-breeding period. Specifically, we examined differences between sexes and among birds originating from three different breeding colonies located south of the APF in the southwest Atlantic Ocean sector of the Southern Ocean. The existence of individual and population-level differences in migration strategies could have repercussions for exposure to anthropogenic threats (e.g., pollutants and fisheries bycatch), or have carryover effects on body condition, behaviour or

performance in the subsequent breeding season, as in other seabird species (Mills et al. 2020, 2021).

## Methods

Feather sampling was undertaken at three brown skua breeding colonies: (1) Esperanza/Hope Bay, Antarctic Peninsula ( $63^{\circ}24'S$ ,  $57^{\circ}01'W$ ) in November/December 2018 and 2019; (2) Signy Island, South Orkney Islands ( $60^{\circ}43'S$ ,  $45^{\circ}36'W$ ) in January 2014; and (3) Bird Island, South Georgia ( $54^{\circ}00'S$ ,  $38^{\circ}03'W$ ) in December 2014. Population sizes at these sites were 26 breeding pairs in 2022/23, 161 breeding pairs in 2013/14 and 467 breeding pairs in 2003/04, respectively (Phillips et al. 2004; Carneiro et al. 2016b; Ibañez, unpublished data). During incubation, adult birds were captured and fully grown body feathers were plucked singly from different parts of the lower back at Bird Island ( $n=26$ ) and Signy Island ( $n=22$ ), and the tip ( $\sim 1$  cm<sup>2</sup>) of a fully grown primary feather (P7 or P8) was sampled at Hope Bay ( $n=45$ ). After collection, feathers were stored dry in sealed polythene bags. Additionally, at Hope Bay only, body feathers were collected from well-grown chicks ( $n=17$ ) in the 2019/20 breeding season. No bird was sampled more than once. Adults were sexed via the analysis of DNA extracted from blood samples at Bird Island, and sexes were initially assigned morphologically (i.e., from weight and tarsus length) at Hope Bay and Signy Island (Fridolfsson and Ellegren 1999; Phillips et al. 2002). Morphological sexing at Hope Bay was later confirmed through DNA analysis.

Brown skuas primarily moult body feathers and outer primary feathers during the non-breeding period (Furness 1987; Phillips et al. 2007; Schultz et al. 2023; but see Graña Grilli and Cherel 2017). Hence, stable isotope ratios of fully grown body feathers and outer primary feathers (both sampled here) are highly likely to reflect diet and distribution during the non-breeding period (Graña Grilli and Cherel 2017; Schultz et al. 2023). Feathers ( $n=3$  pooled per bird) were cleaned of external lipids and contaminants using chloroform:methanol solution (2:1 v/v) and Milli-Q® water rinses. Feathers were then air-dried for 48 h and cut into small fragments with stainless steel scissors. Homogenised feathers were weighed ( $\sim 0.7$  mg) into  $6 \times 4$  mm tin capsules using a microbalance. Stable isotope ratios of carbon and nitrogen were measured at the Natural Environment Isotope Facility Stable Isotope Ecology Lab using a continuous-flow mass spectrometer (Delta Plus XP; Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (vario PYRO cube; Elementar, Langenselbold, Germany). Three internal laboratory standards were analysed for every 10 samples to correct for instrument drift and linearity. Results are expressed as  $\delta$  values (‰) relative to the international references Vienna PeeDee Belemnite and atmospheric  $\text{N}_2$

(AIR) for carbon and nitrogen, respectively. Measurement precision (SDs associated with replicate runs of USGS40) was  $<0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

Data were analysed using R version 4.0.3. and the figure was created using the ggplot2 package in R (Wickham 2016; R Core Team 2020). There was no significant effect of year on adult feather  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at Hope Bay (Wilcoxon rank sum tests, both  $P > 0.08$ ), and hence data were pooled for further analyses. The effects of sex, breeding location and their two-way interaction on feather  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were tested using two-way ANOVAs followed by post hoc Tukey's HSD tests. Statistical significance was assumed at  $\alpha = 0.05$  in all cases. To aid interpretation, we present our data in relation to previously published feather stable isotope data from adult brown skuas from South Georgia and King George Island, and from adult white-chinned petrels *Procellaria aequinoctialis* from South Georgia, which have known non-breeding distributions within the southwest Atlantic Ocean (Phillips et al. 2006, 2007, 2009; Graña Grilli and Chérel 2017).

## Results and discussion

Feather  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of adult brown skuas from our three study populations were highly variable, ranging from  $-20.4$  to  $-15.0\text{‰}$  and  $+7.9$  to  $+19.4\text{‰}$ , respectively (Table 1; Fig. 1), reflecting the large overall distribution during the non-breeding period. There was a significant effect of breeding colony, but not sex, on feather  $\delta^{13}\text{C}$  values (two-way ANOVA, colony:  $F_{2,87} = 14.21$ ,  $P < 0.001$ ; sex:  $F_{1,87} = 0.73$ ,  $P = 0.394$ ; sex  $\times$  colony:  $F_{2,87} = 0.41$ ,  $P = 0.668$ ). There was also a significant effect of breeding colony, but not sex, on  $\delta^{15}\text{N}$  values (log-transformed)

(colony:  $F_{2,87} = 12.73$ ,  $P < 0.001$ ; sex:  $F_{1,87} = 0.11$ ,  $P = 0.738$ ; sex  $\times$  colony:  $F_{2,87} = 2.45$ ,  $P = 0.09$ ). Post hoc Tukey's HSD tests showed that feather  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of birds from South Georgia were significantly lower than those of birds from the other two locations (all  $P < 0.001$ ), which were similar ( $P = 0.10$  and  $P = 0.59$ , respectively).

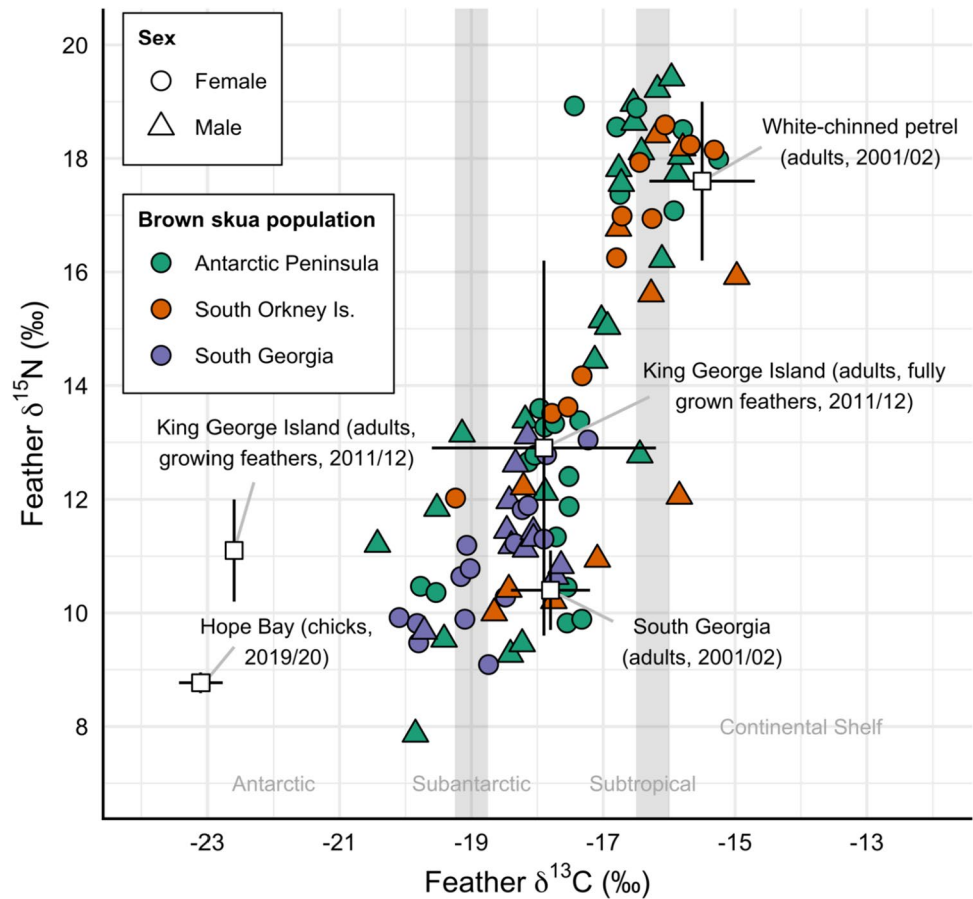
All  $\delta^{13}\text{C}$  values of adult feathers from brown skuas sampled at our three study colonies were greater than the mean  $\delta^{13}\text{C}$  values of chick feathers at Hope Bay (this study) and of growing feathers of adults from King George Island, which were measured by Graña Grilli and Chérel (2017) (Fig. 1). Hence, we infer that no adults from our study spent the non-breeding season in high-latitude Antarctic waters, and that the feathers we sampled were grown outside the breeding period. Previous tracking and stable isotope studies show that brown skuas from South Georgia disperse widely during the non-breeding period, selecting deep, oceanic waters, mostly within the Argentine Basin or elsewhere between the APF and the northern extent of the STF (Phillips et al. 2007, 2009; Carneiro et al. 2016a). Our isotopic data are consistent with this interpretation (i.e., the use of mixed subtropical–subantarctic to subantarctic waters) for the birds that we sampled from South Georgia. However, this interpretation held only for a subset of the birds from Signy Island and Hope Bay, whereas the remainder of the birds sampled at the two high-latitude colonies showed considerably higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, which were more similar to those of white-chinned petrels from South Georgia (Fig. 1). As such, we infer that this subset of brown skuas, like the white-chinned petrels, make extensive use of the Patagonian Shelf and shelf-slope during the non-breeding period (Phillips et al. 2006). This is corroborated by the similar statistical distributions of adult feather isotope data from brown skuas at Hope Bay and Signy Island in our study with previously

**Table 1** Stable isotope ratios (‰) of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) measured in feathers of brown skuas *Stercorarius antarcticus lönnerbergi* sampled from three breeding colonies in the southwest Atlantic sector of the Southern Ocean: (1) Esperanza/Hope Bay, Ant-

arctic Peninsula (primary feather tips; P7 or P8); (2) Signy Island, South Orkney Islands (body feathers); and (3) Bird Island, South Georgia (body feathers)

Breeding location	Age	Sex	n	Feather $\delta^{13}\text{C}$			Feather $\delta^{15}\text{N}$		
				Mean $\pm$ SD	Minimum	Maximum	Mean $\pm$ SD	Minimum	Maximum
Antarctic Peninsula	Adult	Female	22	$-17.5 \pm 1.1$	-19.8	-15.2	$13.8 \pm 3.3$	9.8	18.9
	Adult	Male	23	$-17.5 \pm 1.4$	-20.4	-15.8	$14.6 \pm 3.7$	7.9	19.4
	Adult	Both	45	$-17.5 \pm 1.2$	-20.4	-15.2	$14.2 \pm 3.5$	7.9	19.4
	Chick	–	17	$-23.1 \pm 0.3$	-23.7	-22.5	$8.8 \pm 0.2$	8.5	9.2
South Orkney Is	Adult	Female	11	$-16.8 \pm 1.1$	-19.2	-15.3	$16.0 \pm 2.3$	12.0	18.6
	Adult	Male	11	$-16.9 \pm 1.2$	-18.7	-15.0	$13.7 \pm 3.3$	10.0	18.4
	Adult	Both	22	$-16.9 \pm 1.1$	-19.2	-15.0	$14.9 \pm 3.0$	10.0	18.6
South Georgia	Adult	Female	15	$-18.7 \pm 0.8$	-20.1	-17.2	$10.9 \pm 1.2$	9.1	13.0
	Adult	Male	11	$-18.3 \pm 0.6$	-19.7	-17.6	$11.4 \pm 0.9$	9.7	13.1
	Adult	Both	26	$-18.5 \pm 0.7$	-20.1	-17.2	$11.1 \pm 1.1$	9.1	13.1

**Fig. 1** Stable isotope ratios (‰) of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) measured in body feathers of brown skuas *Stercorarius antarcticus lönnerbergi* originating from Signy Island (South Orkney Islands) and Bird Island (South Georgia), and in primary feather tips (P7 or P8) from Esperanza/Hope Bay (Antarctic Peninsula). Filled white squares are mean ( $\pm$ SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of body feathers from brown skua chicks at Esperanza/Hope Bay (this study, sampled in 2019/20), adult white-chinned petrels *Procellaria aequinoctialis* and brown skuas (sampled in 2001/02) from Bird Island (Phillips et al. 2007, 2009), and brown skuas from King George/25 de Mayo Island (South Shetland Islands, sampled in 2011/12, including growing and fully grown feathers) (Graña Grilli and Cherel 2017). Grey vertical lines and text reflect the approximate locations of biogeographic boundary zones (Phillips et al. 2009)



published data from King George Island (Graña Grilli and Cherel 2017), as well as tracking data from King George Island which showed that adults spent the non-breeding season over the Patagonian Shelf, Argentine Basin and, to a lesser extent, the southern Brazil Shelf (Krietsch et al. 2017). None of the birds from South Georgia in our study showed isotopic values consistent with use of shelf or shelf-slope waters, though a single individual did in a previous study (Phillips et al. 2007). Hence, although this migration strategy occurs in the South Georgia population, it is much rarer than in higher latitude populations.

The drivers of differences in migration strategies among brown skua populations are unknown; however, factors such as the predictability of certain prey, individual specialisation and the levels of inter- and intraspecific competition likely play a role. Variation in non-breeding distributions and habitat use are likely to have repercussions for the relative exposure to anthropogenic threats. For example, birds feeding at lower compared to higher latitudes, or in coastal/benthic versus offshore/pelagic waters, may be more exposed to mercury in their prey (Fitzgerald et al. 2007; Mills et al. 2020; Renedo et al. 2020). In addition, the skuas feeding on the Patagonian Shelf likely show a greater reliance during the nonbreeding season on scavenging offal and discards

from behind vessels, and hence may show higher bycatch rates in trawl fisheries (Paz et al. 2018; Tamini et al. 2021). Moreover, the recent outbreak of Highly Pathogenic Avian Influenza (HPAI) at South Georgia could potentially have originated from a brown skua that wintered off Argentina prior to returning to the colony. If so, this is a rare migration strategy for this population, as one bird in Phillips et al. (2007) but none in our study (as outlined above) had an isotopic signature associated with feeding on the Patagonian Shelf. Given that a high proportion of brown skuas from the Antarctic Peninsula and South Orkneys in our study wintered on the Patagonian Shelf, these populations may also be at risk.

Brown skuas show reversed (i.e., female-biased) sexual size dimorphism (SSD), with females being considerably larger and heavier than males (Phillips et al. 2002). Despite the SSD, there was no significant effect of sex on feather  $\delta^{13}\text{C}$  values, suggesting no consistent differences between males and females in habitat use during the non-breeding period. Similarly, previous tracking studies at South Georgia did not find sex differences in foraging areas (Phillips et al. 2007; Carneiro et al. 2016a). There was also no significant effect of sex on feather  $\delta^{15}\text{N}$  values, which suggests no overall difference in trophic levels between sexes. Nonetheless,

mean  $\delta^{15}\text{N}$  values were slightly higher for males than females at Hope Bay and South Georgia, whereas the opposite pattern was found for birds from Signy Island (Table 1).

## Conclusion

Our study highlighted the diverse migration strategies of brown skuas from different breeding colonies in the south-west Atlantic sector of the Southern Ocean. Birds from all colonies, particularly those from South Georgia, targeted deep, oceanic waters. However, a large proportion from the South Orkneys and the Antarctic Peninsula instead utilised the Patagonian Shelf. Although the factors driving these differences remain unclear, it is likely that different strategies lead to varying ecological and anthropogenic pressures across populations, which underscores the importance of considering such variability in future conservation planning and management. Future work could use isotopic analyses of feathers from adults to analyse annual consistency in the migration strategies of brown skuas (potentially including repeat sampling of the same individuals, or feathers from museum skins), with the caveat that isotopic baselines may also change over time.

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**Author contributions** WFM: conceptualisation; funding acquisition; data curation; project administration; formal analysis; methodology; visualisation; writing—original draft. AEI: conceptualisation; funding acquisition; project administration; methodology; resources; writing—original draft. APBC: resources; writing—review and editing. LMM: resources; writing—review and editing. RMJ: resources; writing—review and editing. RARM: investigation; writing—review and editing. DM: Supervision; writing—review and editing. RAP: conceptualisation; funding acquisition; project administration; resources; methodology; supervision; writing—review and editing.

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**Data availability** Data will be made available from the corresponding authors upon reasonable request.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare.

**Ethical approval** All feather sampling at Bird Island and Signy Island was approved by the British Antarctic Survey Animal Welfare Ethical Review Body and carried out under permit from the Government of South Georgia and the South Sandwich Islands, or the UK government, respectively. At Esperanza/Hope Bay, all applicable international, national and institutional guidelines for sampling, care and experimental use of animals for the study were followed as established by the 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 IAA and Dirección Nacional del Antártico (DNA).

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## References

- Anderson ORJ, Phillips RA, Shore RF, McGill RAR, McDonald RA, Bearhop S (2009) Diet, individual specialisation and breeding of brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. *Polar Biol* 32:27–33
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol Biochem Zool* 75:451–458
- Borghello P, Torres DS, Montalti D, Ibañez AE (2019) Diet of the brown skua (*Stercorarius antarcticus lonnbergi*) at Hope Bay, Antarctic Peninsula: differences between breeders and non-breeders. *Polar Biol* 42:385–394
- Burton RW (1968) Breeding biology of the brown skua, *Catharacta skua lonnbergi* (Mathews), at Signy Island, South Orkney Islands. *Br Antarct Surv Bull* 15:9–28
- Carneiro APB, Manica A, Phillips RA (2014) Foraging behaviour and habitat use by brown skuas *Stercorarius lonnbergi* breeding at South Georgia. *Mar Biol* 161:1755–1764
- Carneiro APB, Manica A, Trivelpiece WZ, Phillips RA (2015) Flexibility in foraging strategies of Brown Skuas in response to local and seasonal dietary constraints. *J Ornithol* 156:625–633
- Carneiro APB, Manica A, Clay T, Silk J, King M, Phillips R (2016a) Consistency in migration strategies and habitat preferences of brown skuas over two winters, a decade apart. *Mar Ecol Prog Ser* 553:267–281
- Carneiro APB, Manica A, Phillips RA (2016b) Long-term changes in population size, distribution and productivity of skuas (*Stercorarius* spp.) at Signy Island. *South Orkney Islands Polar Biol* 39:617–625
- Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122:155–162

- Delord K, Cherel Y, Barbraud C, Chastel O, Weimerskirch H (2018) High variability in migration and wintering strategies of brown skuas (*Catharacta antarctica lonnbergi*) in the Indian Ocean. *Polar Biol* 41:59–70
- Fitzgerald WF, Lamborg CH, Hammerschmidt CR (2007) Marine biogeochemical cycling of mercury. *Chem Rev* 107:641–662
- Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30:116–121
- Furness RW (1987) The skuas. T & AD Poyser, Calton
- Graña Grilli M, Cherel Y (2017) Skuas (*Stercorarius* spp.) moult body feathers during both the breeding and inter-breeding periods: implications for stable isotope investigations in seabirds. *Ibis* 159:266–271
- Graña Grilli M, Montalti D (2015) Variation in diet composition during the breeding cycle of an Antarctic seabird in relation to its breeding chronology and that of its main food resource. *Polar Biol* 38:643–649
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of  $^{13}\text{C}$  in tissues. *Condor* 94:181–188
- Ibañez AE, Morales LM, Torres DS, Borghello P, Montalti D (2022) Pellet analysis evidences flexibility in the diet of Brown Skua (*Stercorarius antarcticus*) during breeding at Esperanza/Hope Bay (Antarctic Peninsula). *Polar Biol* 45:419–426
- Jaeger A, Lecomte VJ, Weimerskirch H, Richard P, Cherel Y (2010) Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Commun Mass Spectrom* 24:3456–3460
- Kopp M, Peter H-U, Mustafa O, Lisovski S, Ritz MS, Phillips RA, Hahn S (2011) South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Mar Ecol Prog Ser* 435:263–267
- Krietsch J, Hahn S, Kopp M, Phillips RA, Peter H-U, Lisovski S (2017) Consistent variation in individual migration strategies of brown skuas. *Mar Ecol Prog Ser* 578:213–225
- Mills WF, Bustamante P, McGill RAR, Anderson ORJ, Bearhop S, Cherel Y, Votier SC, Phillips RA (2020) Mercury exposure in an endangered seabird: long-term changes and relationships with trophic ecology and breeding success. *Proc R Soc b: Biol Sci* 287:20202683
- Mills WF, McGill RAR, Cherel Y, Votier SC, Phillips RA (2021) Stable isotopes demonstrate intraspecific variation in habitat use and trophic level of non-breeding albatrosses. *Ibis* 163:463–472
- Mills WF, Ibañez AE, Bustamante P, Carneiro APB, Bearhop S, Cherel Y, Mariano-Jelicich R, McGill RAR, Montalti D, Votier SC, Phillips RA (2022) Spatial and sex differences in mercury contamination of skuas in the Southern Ocean. *Environ Pollut* 297:118841
- Paz JA, Seco Pon JP, Favero M, Blanco G, Copello S (2018) Seabird interactions and by-catch in the anchovy pelagic trawl fishery operating in northern Argentina. *Aquat Conserv* 28:850–860
- Phillips RA, Dawson DA, Ross DJ (2002) Mating patterns and reversed size dimorphism in southern skuas (*Stercorarius skua lonnbergi*). *Auk* 119:858–863
- Phillips RA, Phalan B, Forster IP (2004) Diet and long-term changes in population size and productivity of brown skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. *Polar Biol* 27:555–561
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol Conserv* 129:336–347
- Phillips RA, Cetry P, Silk JRD, Bearhop S, McGill R, Afanasyev V, Strange IJ (2007) Movements, winter distribution and activity patterns of Falkland and brown skuas: insights from loggers and isotopes. *Mar Ecol Prog Ser* 345:281–291
- Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* 160:795–806
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reinhardt K, Hahn S, Peter H-U, Wemhoff H (2000) A review of the diets of Southern hemisphere skuas. *Mar Ornithol* 28:7–19
- Renedo M, Bustamante P, Cherel Y, Pedrero Z, Tessier E, Amouroux D (2020) A “seabird-eye” on mercury stable isotopes and cycling in the Southern Ocean. *Sci Total Environ* 742:140499
- Ritz MS, Millar C, Miller GD, Phillips RA, Ryan P, Sternkopf V, Liebers-Helbig D, Peter H-U (2008) Phylogeography of the southern skua complex—rapid colonization of the southern hemisphere during a glacial period and reticulate evolution. *Mol Phylogenet Evol* 49:292–303
- Schultz H, Hohnhold RJ, Taylor GA, Bury SJ, Bliss T, Ismar SMH, Gaskett AC, Millar CD, Dennis TE (2018) Non-breeding distribution and activity patterns in a temperate population of brown skua. *Mar Ecol Prog Ser* 603:215–226
- Schultz H, Battley PF, Bury SJ, Chang K, Ismar-Rebitz SMH, Gaskett AC, Dennis TE, Hohnhold RJ, Taylor GA, Scofield RP, Rayner MJ, Tennyson AJD, Hemmings AD, Millar CD (2023) Non-breeding behaviour in the Brown Skua (*Stercorarius antarcticus lonnbergi*): insights from modelling moulting patterns and stable isotope analyses. *Emu Austral Ornithology* 123:49–59
- Tamini LL, Chavez LN, Dellacasa RF, Crawford R, Frere E (2021) Incidental capture of seabirds in Argentinean side-haul trawlers. *Bird Conserv Int* 31:591–604
- Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

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