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ORIGINAL PAPER

Feeding ecology of two congeneric seabirds at the South Shetland Islands, Antarctica

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Abstract

Seabirds play a key role in maintaining the balance and functioning of marine ecosystems. Changing energy demands during reproduction, coupled with prey availability and competition, shape seabird foraging behaviors and diets. Brown Skuas *Stercorarius antarcticus lonnbergi* and South Polar Skuas *S. maccormicki* are opportunistic feeders and scavengers that breed sympatrically on the Antarctic Peninsula and nearby islands. In shared nesting areas, Brown Skuas often monopolize resources on land, compelling South Polar Skuas to exploit alternative trophic pathways at sea. This study investigates the diets of Brown and South Polar Skuas by analyzing regurgitated pellets ($n = 443$) collected during three breeding seasons (2021–2023) and blood stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) sampled in 2021/22 at the Potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica. Pellet analysis showed that Brown Skuas consumed penguins more frequently and had a broader dietary niche compared to South Polar Skuas, which consumed more large, mesopelagic fish (predominantly Antarctic Lanternfish *Electrona antarctica*) and Storm Petrels. As the breeding season progressed, both species increasingly relied on marine resources from incubation to the chick-rearing, indicating dietary plasticity. Blood $\delta^{13}C$ values suggested greater coastal/inshore foraging for Brown Skuas and offshore foraging for South Polar Skuas. Elevated $\delta^{15}N$ values in Brown Skuas indicated a higher trophic level, and their isotopic niche breadth was wider than South Polar Skuas. No sex-related variations were detected in blood isotopic signatures. The dietary diversity, adaptability and the presence of distinct ecological niches likely facilitate skua coexistence during sympatric breeding.

Keywords Seabirds · Stercorarius · Diet · Regurgitated pellets · Stable isotopes · Antarctica

Introduction

Seabirds are globally important marine predators, with an annual biomass consumption of ~70 million tonnes, which is similar to commercial fisheries landings (Brooke 2004). As mid to high trophic level predators, many seabirds species play critical roles in regulating marine food webs and ecosystem dynamics. Seabirds are conspicuous, long-lived species with high adult survival and low reproductive output, making their populations relatively stable over time. Understanding how seabirds use resources, such as through diet studies, can provide insights into the variability in marine food webs resulting from changing environmental conditions, and into the factors driving their breeding success and population dynamics (Furness and Camphuysen 1997; Barrett et al. 2007; Velarde et al. 2019).

Different methodologies are commonly used to study seabirds diets, including analyses of regurgitated pellets, regurgitations, stomach-flushing, as well as biochemical

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methods (e.g., stable isotope and fatty acid analyses) (Duffy and Jackson 1986; Bearhop et al. 2002). Pellets are compact masses of indigestible material (e.g., bones, feathers, otoliths) that are naturally regurgitated by several seabird species. The analysis of pellets offers several advantages, including ease of sample collection, minimal impact on the birds and high taxonomic resolution (i.e., species-level identification of prey); however, this approach underestimates the amount of easily digestible soft-bodied prey (Votier et al. 2003; Malzof and Quintana 2008). Stable isotope ratios of carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) measured in seabird tissues are effective tracers of foraging habitats and trophic levels, respectively, and reflect diet over different temporal scales, depending on the tissue (Bond and Hobson 2012; Layman et al. 2012; Mills et al. 2024). For instance, the isotopic values of blood plasma or serum integrate dietary information over the previous few days (typically 3–5 days), whereas the isotopic signature of red blood cells (RBCs) integrate dietary inputs over a longer period, usually 2–3 weeks (Boecklen et al. 2011; Vander Zanden et al. 2015; Graña Grilli et al. 2023). Combining traditional and biochemical diet analyses provides a more comprehensive approach to investigating seabird trophic ecology (Bearhop et al. 2004; Barrett et al. 2007; Graña Grilli et al. 2023).

Trophic niches of seabirds can vary among and within species, including in relation to intrinsic (e.g., age, sex, individual preferences, experience, breeding stage and season) and extrinsic (e.g., competition, prey availability and accessibility) factors (Bolnick et al. 2003; Carneiro et al. 2015; Phillips et al. 2017). Moreover, even within populations of generalist species sharing the same environment, individuals often exhibit specialist foraging strategies (Jakubas et al. 2018; Gal et al. 2021). Trophic niche partitioning can reduce competition and facilitate coexistence among morphologically similar sympatric seabird species, especially during the breeding period when seabirds behave as central-place foragers and are restricted in their efforts (in time and distance from the colony) (Orians and Pearson 1979; Robertson et al. 2014; Petalas et al. 2021). While rearing chicks, adult seabirds must adapt their foraging strategies and diets to manage the energy requirements of themselves and their chicks alongside seasonal fluctuations in prey accessibility and availability (Shaffer et al. 2003; Hipfner et al. 2013; Ibañez et al. 2022).

Brown Skuas *Stercorarius antarcticus lonnbergi* and South Polar Skuas *S. maccormicki* breed on the Antarctic continent and subantarctic islands. Both species display circumpolar breeding distributions, though Brown Skuas mainly breed on subantarctic islands and South Polar Skuas on the Antarctic continent (Young 1994; Ritz et al. 2008). Skuas can be top predators, scavengers and kleptoparasites, and their diets include a wide variety of food resources on land and at sea (Reinhardt and Hahn 2000; Borghello et al. 2019; Ibañez et al. 2022). In the Antarctic Peninsula region and the South Shetland Islands, there is an overlap in the breeding distributions of these skua species (Furness 1987; Pietz 1987; Ritz et al. 2006). Both species breed nearby penguin colonies in the northern Antarctic Peninsula region – a food resource that they can defend territorially – and also have access to the sea (Trillmich 1978; Trivelpiece et al. 1980; Hahn and Peter 2003). When breeding in sympatry, Brown Skuas initiate their breeding cycle, particularly egg incubation, in close synchrony with that of penguins, which facilitates their monopolization of this prey (eggs and chicks) and other seabirds, thereby forcing South Polar Skuas to feed in inshore and offshore pelagic waters (Malzof and Quintana 2008; Graña Grilli and Montalti 2012; Reis et al. 2021). Nevertheless, when sympatry occurs in a context of limited availability of penguin, and high energy demands, both species supplement their diet with other resources (Graña Grilli and Montalti 2012; Carneiro et al. 2015; Ibañez et al. 2022). This study investigated the feeding ecology of both skuas during three consecutive breeding seasons, considering the effects of sex, breeding stage and season. Furthermore, the combination of stable isotope and regurgitated pellets analyses demonstrates the utility of combining methods to understand seabird diets and foraging strategies. The central hypothesis here is that, under the specific conditions of the study site, Brown Skuas monopolizes the most highly valued resource, the penguin colony.

Materials and methods

Study area

Fieldwork was conducted at the Potter Peninsula, Isla 25 de Mayo (King George Island), South Shetland Islands, Antarctica (62°15’S, 58°40’W), part of which is included as Antarctic Specially Protected Area (ASPA) no. 132, during the breeding seasons 2020/2021, 2021/2022, and 2022/2023 (Fig. 1). At this site, Brown Skua pairs (2021/2022: $n=17$; 2022/2023: $n=19$), South Polar Skua pairs (2021/2022: $n=87$; 2022/2023: $n=80$), and mixed pairs (composed of one adult of each species or hybrid individuals; 2021/2022: $n=5$; 2022/2023: $n=11$) breed in sympatry. A limited number of pairs remained uncategorized in each year, as only one member of the pair was seen (2021/2022: $n=15$; 2022/2023: $n=13$). Individuals were classified as Brown or South Polar Skuas based on their coloration and morphology (Parmelee 1988; Peter et al. 1990), and only active pairs composed of two individuals of the same species were included in this study. At the Potter Peninsula, there are

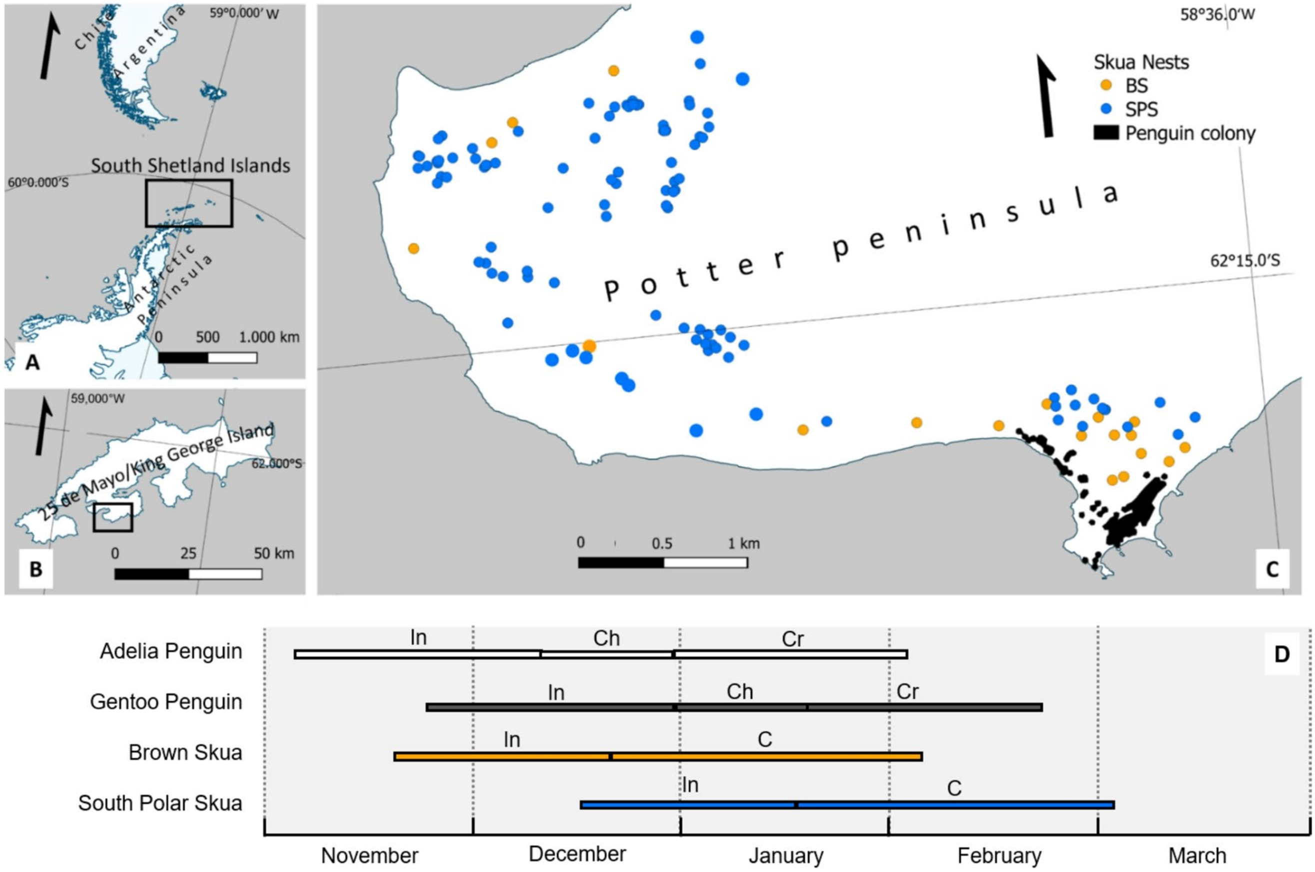

Fig. 1 Spatial and temporal distribution of skuas species during breeding season. (**A**) Study area within the southwest Atlantic sector of the Southern Ocean. (**B**) Location of Potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica (62°15'S, 58°40'W). (**C**) Brown Skua *Stercorarius antarcticus lonnbergi* (BS) and South Polar Skua *S. maccormicki* (SPS) nests identified during the 2022/2023 season. Maps were created using the Quantarctica 3.2 package (Matsuoka et al. 2021) in QGIS 3.16. (**D**) Reproductive chronology of Pygoscelid penguin species and skuas at the Potter Peninsula. Breeding stages are indicated as follows: incubation (In) for both penguins and skuas; parental chick care (Ch) and creche (Cr) for penguins only; and chick-rearing (C) for skuas only

colonies of pygoscelid penguins, comprising ~ 1700 pairs of Adélie Penguins *Pygoscelis adeliae*, ~ 6700 pairs of Gentoo Penguins *P. papua* and ~ 10 pairs of Chinstrap Penguins *P. antarcticus* (Albarrán et al. 2024). There are also other seabirds, which are potential prey of skuas, including Wilson's Storm Petrel *Oceanites oceanicus*, Black-bellied Storm Petrel *Fregetta tropica*, Southern Giant Petrel *Macronectes giganteus*, Cape Petrels *Daption capense* and Antarctic Tern *Sterna vittata* (Aguirre 1994; Hahn et al. 1998; Ausems et al. 2023). On the coasts, Southern Elephant Seals *Mirounga leonina* and Antarctic Fur Seals *Arctocephalus gazella* can be found and serve as prey in the form of carrion (Daneri et al. 2005, 2015; Lanusse et al. 2022).

Sample collection

All active skua nests were monitored every 3–4 days throughout the breeding season, where regurgitated pellets were collected and the reproductive stage of the nest was recorded (In: incubation and C: chick-rearing). It was not possible to determine the specific stage for pellets from the 2020/2021 season; therefore, they were excluded from subsequent analyses comparing stages. To ensure pellets were from the current season and correctly assigned to each stage, those from the start of the season and first monitoring after hatching were removed. Pellets systematically collected from the ground surrounding each nest site during the In stage (mid-November for Brown Skua and mid-December for South Polar Skua) and during the C stage, from egg hatching (late December for Brown Skua and mid-January for South Polar Skua) until chicks were completely feathered (~ 40 days old), including only those clearly assignable to a defended nesting area (Fig. 1). Because of low reproductive success, particularly for South Polar Skuas, many pairs failed during the In stage, resulting in fewer pellets collection, especifically from the C stage. Besides, Brown Skuas produce well-formed, compact pellets that are less prone to disintegration, allowing larger sample sizes to be collected. Pellets were dried in the laboratory and stored in sealed plastic bags for subsequent analysis.

During the season 2021/2022 only, Brown Skuas ($n=26$) and South Polar Skuas ($n=37$) were captured during early In (10–15 days after clutch completion). Individuals were either captured directly while sited on the nest, or by using a noose placed on the ground near the nest. Handling time per individual did not exceed 10 min to minimize stress. Nests were only selected for capture when both adults were present, ensuring that nest protection (eggs and chicks) was never compromised during the procedure. Blood samples (~2 mL) were extracted from the brachial vein using 23-G needles. Samples were kept at 4 °C for approximately 5 h, and then centrifuged for 10 min at 2,000 rpm to separate RBCs and serum, and subsequently stored at −20 °C. Serum and RBCs were then lyophilized and homogenised for isotopic analysis. RBCs was also used for molecular sexing (Fridolfsson and Ellegren 1999). Occasionally, when spontaneous regurgitates (i.e., undigested food items expelled during chick feeding or as a stress response) were observed during fieldwork (e.g., after capture), their contents were registered for descriptive purposes, but these were not collected.

Pellet analysis

Pellet dimensions were measured and volume calculated as: $V=3⁄4\ \pi \times (a \times b \times c)$, where a, b and c are the length, height and width axes, respectively (Borghello et al. 2019). Some pellets were disassembled and could not be measured. Pellets were disaggregated into a Petri dish, contents were analyzed with a binocular microscope (×4) and items were sorted into five categories using published guides and reference material. These categories were: *Pygoscelis* spp.; Teleostei; Aves (excluding penguins); Invertebrata and Mammalia. Non-food items (e.g., rocks, algae and lichens) were excluded from analyses. Items were also further classified as being obtained on land, hereafter "terrestrial" (including *Pygoscelis* spp., Aves and Mammalia), or marine prey (Teleostei and Invertebrata). The *Pygoscelis* spp. and terrestrial prey categories were analyzed both with and without penguin feathers. This distinction was made because penguin feathers are highly abundant, potentially biasing statistical analyses, and because their consumption has been suggested to reflect scavenging behavior and may also serve for pellet formation and antiparasitic function rather than a strictly trophic one (Piersma and Van Eerden 1989). Otoliths were identified, mostly to species level, based on their shape (Hecht 1987). Lengths and masses of fish were estimated from otolith lengths (OLs) measured using a binocular microscope (×6) with an incorporated scale, and specific equations for each fish species were used (Hecht 1987). Bird bones and eggshell remains were identified by comparison with reference material preserved in the Ornithological Collection of the La Plata Museum, Natural Science Faculty and Museum, La Plata National University, Argentina. Mammals and invertebrates were identified according to published guides (Xavier and Cherel 2009; Reid 2016; Schories and Kohlberg 2016; Xavier et al. 2020). Results are expressed as frequency of occurrence (FO), according to the equation $FO = (fi/N)$, where fi is the number of pellets containing item i, and N is the total number of pellets (Duffy and Jackson 1986).

Stable isotope analysis

Given the timing of sampling and isotopic turnover rates, serum isotope values predominantly reflect diet during early In, while RBCs isotope values mainly integrate diet during both early In and late pre-laying periods (Hobson and Clark 1993; Bearhop et al. 2002). Stable isotope values of carbon and nitrogen were determined in serum and RBCs using a continuous-flow system consisting of an elemental analyzer (Flash 2000, Thermo Scientific, Milan, Italy) equipped with the smart EA option and an autosampler (Zero Blank, Costech, Valencia, CA, United States) in the laboratory Littoral Environnement et Sociétés (La Rochelle Université, France). The elemental analyzer was connected via a Conflo IV peripheral to a Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Results were expressed using the conventional delta (δ) notation in per mil (‰) and normalized using a two-point calibration against the international standards Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric N_2 (AIR) for nitrogen (Coplen 2011). The measurement data were obtained using the instrumental software Isodat 3.0 (Thermo Scientific, Bremen, Germany). Accuracy and precision were assessed using certified reference materials USGS-61 (δ^{13}C: -35.05 ± 0.04‰; δ^{15}N: -2.87 ± 0.04‰) and USGS-63 (δ^{13}C: -1.17 ± 0.04‰; δ^{15}N: $+37.83 \pm 0.06$‰) (US Geological Survey, Reston, VA, USA). Measurement errors were <0.10‰ for both δ^{13}C and δ^{15}N values.

Data analysis

Regurgitated pellets

Data processing and analysis was conducted using R (version 4.2.1, R Core Team 2022). Significance was assumed at $\alpha=0.05$ in all cases. Variation in pellet volume was modeled using generalized linear models (GLMs; Gamma distribution and a log link function). Two models were fitted: (1) a model including all seasons, species and their two-way interaction; and (2) a model restricted to seasons 2021/2022 and 2022/2023, to evaluate the effects of season, species, breeding stage and two-way interactions. To evaluate differences in the FO of prey, binomial GLMs were fitted for each diet category, considering the effects of skua species, season and their two-way interaction. Similarly, separate GLMs were fitted for marine and terrestrial prey (as groups) to compare the FO across skua species, breeding stages, and their two-way interactions. Regarding penguin FO and terrestrial prey (as a group), separate models were run including and excluding feathers. All models assumptions were verified using diagnostic plots and residual analyses.

Differences in total length and mass of fish species were evaluated using a Welch's t-test to compare consumption between skua species. The normality of variances was first assessed using the Shapiro-Wilk test. We focused on Antarctic Lanternfish *Electrona antarctica* consumption because sample sizes for Antarctic Silverfish *Pleuragramma antarcticum* were insufficient.

To estimate the overall diet diversity of each species, seasons and during each breeding stage, the trophic niche breadth was calculated using the Levin's index (B) and the Standardized Levin's index (BA), following the formulas $B = 1/\Sigma p_i^2$, where p_i is the proportion of individuals consuming resource i, and $BA = (B-1)/(n-1)$, where n is the total number of food items (Levins 1968; Colwell and Futuyma 1971; Krebs 1999). Additionally, the percentage niche overlap between seasons and species was calculated as: $O\% = [\Sigma p_i q_i/(\Sigma p_i^2\ \Sigma q_i^2)^{1/2}] \times 100$, where pi is the proportion of individuals of one species consuming item i, and qi is the proportion of individuals of the other species consuming the same item (Colwell and Futuyma 1971; Krebs 1999).

Stable isotopes

Two-way ANOVAs were used to assess variation in δ^{13}C and δ^{15}N values of serum and RBCs according to species, sex and their interaction. Isotopic niches were estimated considering the species and the sex of the individuals. Assumptions of normality, homogeneity of variances, and independence were checked before analysis.

Analysis involved standard bivariate ellipses (SEA) with a small-sample-size correction applied via maximum likelihood (SEAc) with the Stable Isotope Bayesian Ellipses in R (SIBER) package in R (Jackson et al. 2011). SEAc is a bivariate analogue of the standard deviation and encompasses ~40% of the data. The isotopic niche was also described using Bayesian Standard Ellipse Areas (SEAb), which estimate the posterior distribution of ellipse areas for each group. SEAb were summarized as the mode of the posterior distribution with 95% credible intervals, providing a measure of central tendency and uncertainty. Overlaps between SEAb and SEAc of species and sexes were calculated as proportions by dividing the areas of overlap by the total areas of the groups being compared. Statistical comparison of isotopic niche size was considered the posterior probability that one condition exceeded another was greater than 0.95, corresponding to an $\alpha = 0.05$ threshold for a one-tailed test (Jackson and Parnell 2023).

Results

Pellet analysis

A total of 443 pellets were collected (Table 1), from Brown (7, 16, and 13 nests) and South Polar Skuas (5, 28, and 8 nests) in 2020/2021, 2021/2022, and 2022/2023, respectively. South Polar Skuas produced significantly smaller pellets than Brown Skuas (GLM, $p < 0.001$), and pellet volumes were lower in the 2021/2022 and 2022/2023 seasons compared to 2020/2021. Furthermore, breeding stage explained more variation in pellet volume than species; volumes were consistently higher during In than during C stage in both species ($p < 0.05$), whereas no significant differences between species were detected in this subset. No significant interaction terms were found in either GLM.

A total of 838 food items from Brown Skua and 208 from South Polar Skua were identified (Table 1). In both species, prey remains belonging to the five categories were observed, with a high contribution of *Pygoscelis* spp., followed by Teleostei. In South Polar Skua, Mammalia category had only one observation in the season 2020/2021. The GLMs revealed that only the categories Teleostei and *Pygoscelis* spp. (excluding feathers) showed significant responses to the predictors (Table S1). Brown Skuas exhibited a significantly higher FO of penguins (excluding feathers) compared to South Polar Skuas ($p < 0.001$). Furthermore, based on the GLM including all three study seasons, the FO of these prey items significantly decreased across years in both species ($p < 0.05$), except for South Polar Skuas in 2022/2023, which did not follow this decreasing trend. GLMs indicated that South Polar Skuas consumed a significantly higher FO of fish compared to Brown Skuas (Table S1). Neither season nor the interaction between species and season had a significant effect on fish FO, suggesting that the interspecific difference in fish consumption is stable across years. There were no significant effects of species or season in GLMs considering *Pygoscelis* spp. with feathers, Aves, Mammalia, and Invertebrata. The categories with penguin feathers and invertebrates could not be reliably estimated, as they were either consistently present or absent within groups, preventing model estimation. In both species, the FO of marine and terrestrial resources (analysed as groups and excluding penguin feathers) were significantly lower during the

Table 1 Number (N) and frequency of occurrence (FO) of food categories (in bold) and particular dietary items found in the regurgitated pellets of breeding brown Skuas *Stercorarius antarcticus lonnbergi* (BS) and South Polar Skuas *S. maccormicki* (SPS) at potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica, during the breeding seasons 2020/2021, 2021/2022 and 2022/2023

	2020/2021				2021/2022				2022/2023			
	BS (*n* = 61)		**SPS** (*n* = 20)		**BS** (*n* = 152)		**SPS** (*n* = 50)		**BS** (*n* = 144)		**SPS** (*n* = 16)	
	N	FO	N	FO	N	FO	N	FO	N	FO	N	FO
***Pygoscelis*spp.**	61	1.00	13	0.65	146	0.96	39	0.78	137	0.95	15	0.94
Adult bones	9	0.15	0	0.00	13	0.09	0	0.00	4	0.03	0	0.00
Chick bones	25	0.41	0	0.00	15	0.10	0	0.00	9	0.06	0	0.00
Indeterminate bones	6	0.10	0	0.00	41	0.27	3	0.06	33	0.23	1	0.06
Eggshell	31	0.51	0	0.00	32	0.21	1	0.02	29	0.20	1	0.06
Feather	60	0.98	13	0.65	133	0.88	39	0.78	130	0.90	15	0.94
Down feather	7	0.11	3	0.15	19	0.13	2	0.04	34	0.24	4	0.25
Teleostei	16	0.26	16	0.80	50	0.33	32	0.64	50	0.35	10	0.63
Bones	14	0.23	15	0.75	47	0.29	24	0.48	43	0.30	6	0.38
Otoliths	2	0.03	5	0.25	9	0.06	22	0.44	13	0.09	7	0.44
Crystallines	1	0.02	2	0.10	1	0.01	10	0.20	1	0.01	3	0.19
Scales	0	0.00	4	0.20	0	0.00	0	0.00	0	0.00	0	0.00
Aves	7	0.11	3	0.15	11	0.07	13	0.26	16	0.12	1	0.06
Bones	5	0.08	3	0.15	9	0.06	11	0.22	10	0.07	1	0.06
Eggshell	2	0.03	0	0.00	1	0.01	0	0.00	7	0.05	0	0.00
Feather	0	0.00	1	0.05	4	0.03	5	0.10	2	0.01	0	0.00
Invertebrata	0	0.00	0	0.00	14	0.09	2	0.04	11	0.08	4	0.25
Gastropoda	0	0.00	0	0.00	9	0.06	0	0.00	9	0.06	3	0.19
Cephalopoda	0	0.00	0	0.00	4	0.03	0	0.00	0	0.00	1	0.06
Crustacea	0	0.00	0	0.00	1	0.01	2	0.04	2	0.01	0	0.00
Mammalia	2	0.03	1	0.05	4	0.03	0	0.00	6	0.04	0	0.00
Fur	2	0.03	1	0.05	4	0.03	0	0.00	6	0.04	0	0.00
Diet categories	86		33		225		86		220		30	
Dietary ítems	164		47		342		119		332		42	

The number of pellets analysed per species are indicated in parentheses. The Aves category excluded Penguins incubation stage compared to the chick-rearing stage (Table S3). Contrarily, when including penguin feathers, the FO of terrestrial prey did not differ significantly between breeding stages (Table S3). Additionally, a non-significant trend towards a higher consumption of marine resources in South Polar Skuas relative to Brown Skuas was observed, whereas Brown Skuas seem to consume more terrestrial prey when feathers were included (Fig. 2).

A total of 180 otoliths were collected from the pellets (Table 2), and Antarctic Lanternfish, Antarctic Silverfish and *Gymnoscopelus* sp. were identified, with Antarctic Lanternfish being most frequent in all cases. Only 10 otoliths could not be identified, which were broken or eroded. Antarctic Lanternfish consumed by South Polar Skua were significantly larger in length (Brown Skua = 88.15 ± 8.71 mm; South Polar Skua = 91.52 ± 7.34 mm) and mass (Brown Skua = 9.52 ± 2.75 g; South Polar Skua = 10.58 ± 2.57 g) than those consumed by Brown Skua (Welch's t-tests, t = 2.38, $p < 0.05$ and t = 2.28, $p < 0.05$). Descriptive statistics for total length and mass of Antarctic Lanternfish and Antarctic Silverfish are presented (Table S2). Otoliths of *Gymnocopelus* sp. were fragmented only allowing the identification at the genus level.

Avian species were identified to genus or species level (Table 2), with most remains belonging to Storm Petrels. Egg remains belonged to skuas and, in one case, to Southern Giant Petrel. Remains of birds from the vicinity of the nests were collected, and Wilson's Storm Petrel and Black-bellied Storm Petrel were identified, along with some species not represented in the pellets: Snowy Sheathbill *Chionis alba*, Kelp Gull *Larus dominicanus*, Blue Petrel *Halobaena caerulea* and Snow Petrel *Pagodroma nivea* (excluded from Table 2).

Within the Mammalia category, Southern Elephant Seal and Antarctic Fur Seal remains were observed. Invertebrata species comprised Antarctic Krill *Euphausia superba* and Antarctic Limpet *Nacella concinna* (Table 2). Unidentified invertebrate items included one gastropod shell sample and five squid beaks.

The Standardized Levin's Index (BA) was higher in South Polar Skuas (0.43) than in Brown Skuas (0.28). Niche overlap between species was 80.97%, 92.14%, and 96.03% in the 2020/2021, 2021/2022, and 2022/2023 seasons, respectively, with an overall overlap of 92.3%. When penguin feathers were excluded as prey, the pattern reversed: Brown Skuas showed a higher BA (0.42) than South Polar Skuas (0.35), and the total trophic overlap decreased to 70.2%, with lower values in each season (51.27%, 63.30%, and 89.29%). Across breeding stages, BA increased from incubation to chick-rearing in both species, with a stronger change in Brown Skuas (In = 0.19, C = 0.34) than in South Polar Skuas (In = 0.43, C = 0.44). Excluding feathers, the same pattern was observed but with smaller differences (Brown Skua: In = 0.44, C = 0.45; South Polar Skua: In = 0.38, C = 0.40). Finally, Brown Skuas showed a steady increase in BA across seasons (including feathers: 0.21, 0.27, 0.31; excluding feathers: 0.28, 0.41, 0.50). South Polar Skuas exhibited a similar increasing trend when feathers

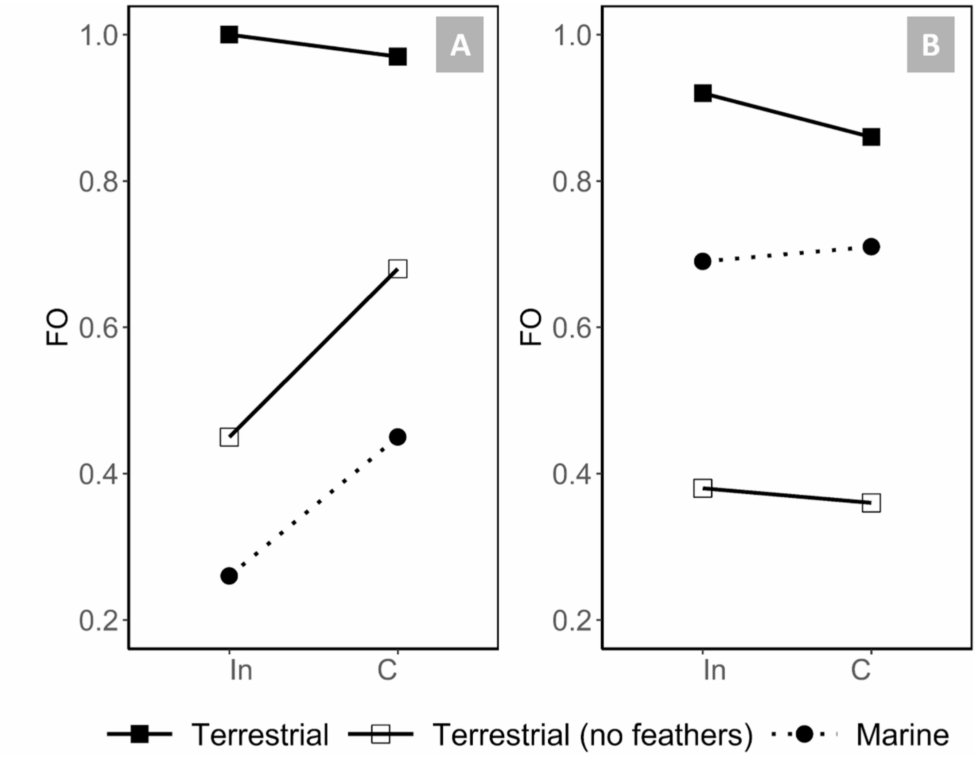

Fig. 2 Frequency of occurrence (FO) of prey obtained on land ("terrestrial"; squares and solid lines, including penguin, flying birds and mammal items) and marine prey (circles and dotted lines; including fish and invertebrates items) consumed during the incubation (In) and chick-rearing (C) by Brown Skuas *Stercorarius antarcticus lonnbergi* (**A**) and South Polar Skuas *S. maccormicki* (**B**), from Potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica, over three consecutive breeding seasons (2021–2023). Data are presented with penguin feathers included (fill squares) and excluded (empty squares) as a prey item

Table 2 Identification of prey species consumed from regurgitated pellets analysis. Prey species consumed by brown Skua *Stercorarius antarcticus lonnbergi* (BS) and South Polar Skua *S. maccormicki* (SPS) from potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica, over three consecutive breeding seasons (2021–2023), identified from prey remains found in pellets: otoliths for Teleostei, bone fragments, feathers and eggshell fragments for Aves

	2020/2021		2021/2022		2022/2023	
Species	BS	SPS	BS	SPS	BS	SPS
Teleostei						
Electrona antarctica	4	17	25	66	22	22
Pleuragramma antarcticum	0	1	2	7	0	0
Gymnoscopelus sp.	0	0	0	3	1	0
Unidentified	2	1	1	2	1	3
Aves						
Oceanites oceanicus	1	0	2	5	4	0
Fregetta tropica	0	1	3	3	1	1
Storm petrel unid.	1	1	3	2	4	0
Stercorarius sp	0	0	1	1	2	0
Sterna vittata	1	0	0	0	0	0
Macronectes giganteus	0	0	0	0	1	0
Daption capense	0	1	0	0	1	0
Pachyptila sp.	0	0	0	1	0	0
Unidentified	5	0	2	2	5	0
Invertebrata						
Nacella concinna	0	0	9	0	8	3
Euphausia superba	0	0	1	2	2	0
Unidentified	0	0	4	0	1	1
Mammalia						
Mirounga leonina	0	0	2	0	2	0
Arctophoca gazella	2	1	2	0	4	0

Mammalia were identified by the hair characteristics, and invertebrata by exoskeletons or beaks. The Aves category excluded Penguins

were excluded (0.23, 0.32, 0.47), but not when they were included (0.38, 0.43, 0.41).

Spontaneous regurgitates

A total of 22 spontaneous regurgitates (excluded from the quantitative analyses presented in tables and figures) were observed and described across the three breeding seasons (Brown Skua: $n=9$, South Polar Skua: $n=13$). Penguin remains (feathers and viscera) were exclusively found in Brown Skua regurgitates ($n=4$). Fish were a prevalent component, particularly in South Polar Skua regurgitates (Brown Skua: $n=3$, South Polar Skua: $n=11$). Krill was present in both species (Brown Skua: $n=3$, South Polar Skua: $n=2$), often co-occurring with fish. Less frequent items included feathers, potentially of a Storm Petrel ($n=2$), and a single occurrence of the giant deep-sea amphipod *Eurythenes gryllus* in a South Polar Skua regurgitate.

Stable isotope analysis

Mean values of δ^{13}C and δ^{15}N in RBCs and serum are presented in Table 3. Interspecific differences were significant for δ^{13}C and δ^{15}N in RBCs (two-way ANOVAs, $F=73.8$, $p<0.0001$ and $F=9.9$, $p<0.01$). Serum δ^{13}C, but not δ^{15}N values, was significantly different between species ($F=44.4$, $p<0.0001$ and $F=3.5$, $p=0.07$). There were no sex differences in the δ^{13}C and δ^{15}N values of RBCs ($F=2.91$, $p=0.09$ and $F=2.88$, $p=0.10$) or serum ($F=0.575$, $p=0.45$, $F=1.22$, $p=0.27$). No interaction terms were significant (all $p\geq 0.79$).

The intraspecific overlap in SEAb between male and female Brown Skua was 40.7% in serum and 39.9% in RBCs, whereas in South Polar Skua, it was 35% and 17.2%, respectively. At the interspecific level, no overlap was detected in SEAc for RBCs, and only a minimal overlap (0.03%) was observed in serum (Fig. 3). In contrast, SEAb revealed greater interspecific overlap, with 9.6% in serum and 18.2% in RBCs (Table S4). Highest sex-specific interspecific overlaps in SEAb occurred between females of both species (11.2% in serum; 21.1% in RBCs), and between male Brown Skuas and female South Polar Skuas (8.9% in serum; 26.9% in RBCs) (Table S4). The isotopic niche breadth of Brown Skua was significantly greater than that of South Polar Skua in both RBCs and serum (Fig. 3). Significant sex-related differences in isotopic niche were only detected in South Polar Skuas, with females exhibiting higher values than males (Table 3).

Table 3 Mean (± SD) stable isotope values (‰) of carbon (δ^{13}C) and nitrogen (δ^{15}N) in red blood cells (RBC) and serum from brown Skuas *Stercorarius antarcticus lonnbergi* (BS) and South Polar Skuas *S. maccormicki* (SPS) from potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica, during the 2021/2022 breeding season

Species	Tissue	Sex	*n*	δ^{13}C (‰)	$\delta^{15}N$ (‰)	SEAc (‰^{2})	SEAb (‰^{2})
BS	Serum	-	26	–22.8 ± 1.6	11.8 ± 1.0	-	-
		Male	14	–22.8 ± 1.7	11.9 ± 1.1	6.06	5.29 [3.07, 9.48]
		Female	12	–22.8 ± 1.5	11.7 ± 0.9	4.73	4.08 [2.24, 7.65]
	RBC	-	26	–22.2 ± 1.1	11.8 ± 1.2	-	-
		Male	14	–22.1 ± 1.2	12.1 ± 1.3	4.52	2.86 [1.60, 5.36]
		Female	12	–22.3 ± 1.0	11.5 ± 1.0	3.36	3.99 [2.31, 7.11]
SPS	**Serum**	-	37	–24.7 ± 0.5	12.2 ± 0.3	-	-
		Male	18	–24.9 ± 0.4	12.3 ± 0.3	0.28	0.26 [0.17, 0.44]
		Female	19	–24.5 ± 0.5	12.0 ± 0.3	0.55	0.49 [0.32, 0.81]
	RBC	-	37	–24.1 ± 0.8	11.2 ± 0.4	-	-
		Male	18	–24.5 ± 0.4	11.3 ± 0.2	0.23	0.21 [0.13, 0.36]
		Female	19	–23.8 ± 0.9	11.0 ± 0.5	1.13	1.07 [0.67, 1.73]

Standard ellipse areas (‰^{2}) corrected for small samples sizes (SEAc) and the mode and 95% credible intervals for bayesian standard ellipse areas (SEAb, ‰^{2}) are shown

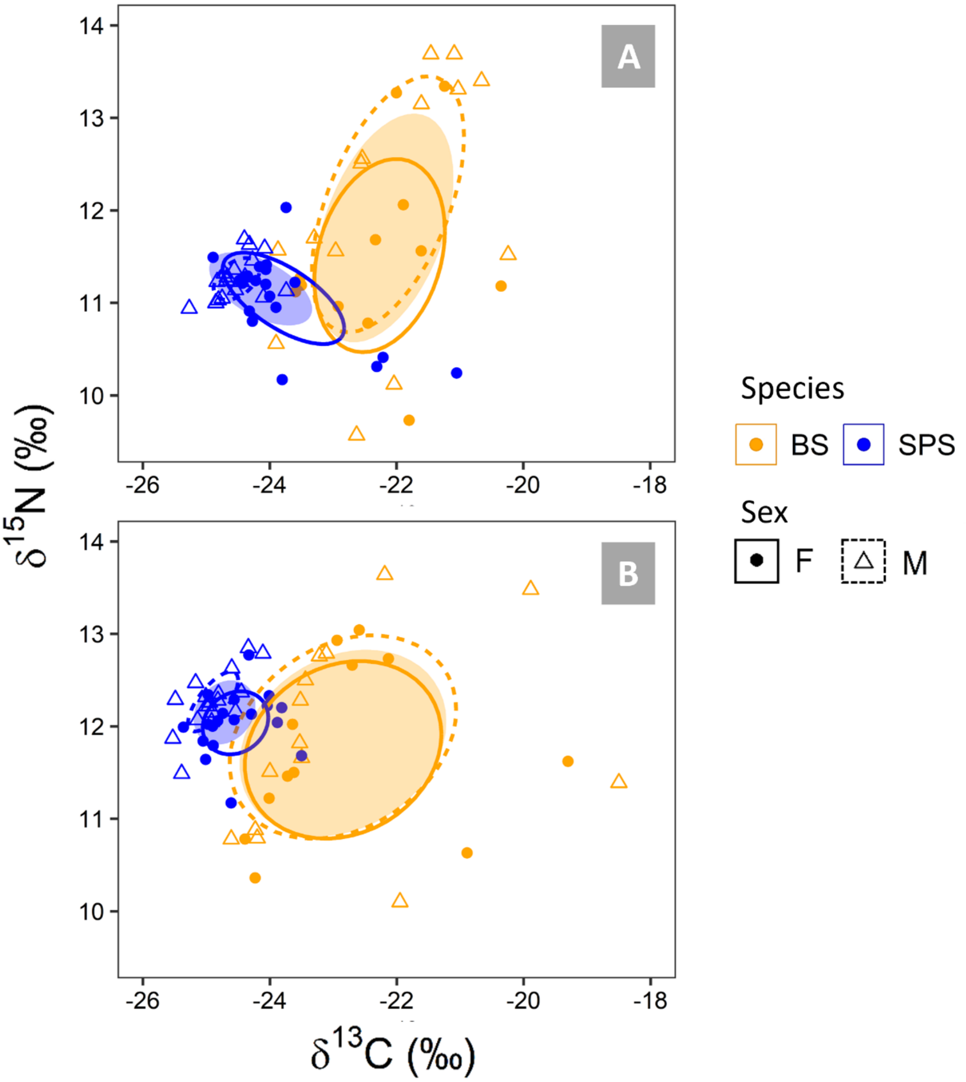

Fig. 3 Individual stable isotope values (‰) of carbon (δ^{13}C) and nitrogen (δ^{15}N) measured in the serum (**A**) and red blood cells (**B**) of Brown Skuas *Stercorarius antarcticus lönnbergi* (BS) and South Polar Skuas *S. maccormicki* (SPS) from Potter Peninsula, 25 de Mayo/King George Island, South Shetland Islands, Antarctica, during the 2021/2022 breeding season. Lines indicated the Standard Ellipse Areas corrected for small sample size (SEAc) for males (M; triangles and dashed lines) and females (F; circles and solid lines) of each species. Additionally, the filled ellipses without contours represent the SEAc for each species without distinguishing between sexes

Discussion

Diet of Skuas based on regurgitated pellets

Analysis of regurgitated pellets indicated interspecific differences in Brown Skua and South Polar Skua diet at the South Shetland Islands. The two species differed significantly in their consumption of *Pygoscelis* spp. (excluding feathers) and Teleostei (Table 1 and S1). Brown Skua exhibited a significantly higher preference for penguins, whereas South Polar Skua showed a significantly greater consumption of fish. These results are in line with previous studies in areas of sympatry for these species, where Brown Skua and South Polar Skua feed mostly on resources obtained on land (land-breeding penguins or other seabirds) and pelagic marine resources, respectively (Pietz 1987; Malzof and Quintana 2008; Graña Grilli and Montalti 2012). This pattern may be attributed to the competitive exclusion of South Polar Skua from terrestrial and most abundant resources by Brown Skua due to their greater size and aggressiveness (Burton 1968; Trivelpiece and Volkman 1982; Pietz 1987; Graña Grilli and Montalti 2012). Similarly to other Antarctic locations, at the Potter Peninsula, Brown Skua nest near penguin colonies (Fig. 1), which increases their ability to monopolize and access this resource (Malzof and Quintana 2008; Graña Grilli and Montalti 2012; Ibañez et al. 2022). Penguin colonies serve as a primary food source for many breeding skua populations (Young 1994; Emslie et al. 1995; Borghello et al. 2019). Due to their abundance, mass and high energy content, penguins provide a more valuable food source for breeding skuas compared to fish, which require longer and costly, in terms of energy expenditure, foraging trips (Norman et al. 1994; Votier et al. 2004). In line with this, the breeding cycle of Brown Skua overlaps with that of Pygoscelid penguins (Ibañez et al. 2022), and they begin the incubation stage earlier than South Polar Skua in the season, therefore increasing their ease of monopolizing these areas and resource (Fig. 1). Breeding allochrony is therefore another factor that contributes to the differences in diet composition at the South Shetland Islands.

Competition for penguins can depend on their abundance, as well as the number of skuas competing for this prey (Colwell and Futuyma 1971; Votier et al. 2007; Dehnhard et al. 2020). When penguin abundance or accessibility is low, both Brown Skua and South Polar Skua supplement their diet with other prey, such as fish, flying seabirds, mammal and invertebrates (Malzof and Quintana 2008; Ibañez et al. 2022). The consumption of penguins by both skua species decreased across the seasons (except for South Polar Skuas in the 2022/2023 season), which may be related to a decline in the penguin colony at Potter Peninsula, increasing competition for this resource and forcing the skuas to exploit alternative food sources (Sander et al. 2007). Additionally, Brown Skua pairs hold feeding territories with an optimal ratio of one skua pair to 766 penguin pairs (Trivelpiece et al. 1980; Hahn and Peter 2003). At the study site, the penguin colony is constituted by 8450 breeding pairs (considering the three *Pygoscelis* species) (Albarrán et al. 2024), reflecting a low skua-penguin ratio (1:70). In this scenario, penguins may represent a resource with limited availability for skuas, which ultimately may force them to use alternative resources (Ibañez et al. 2022). However, for both species, penguins remained the most frequent prey found in pellets (Table 1). Penguin bones and eggshell remains were present almost exclusively in Brown Skua pellets, whereas South Polar Skua pellets predominantly contained feathers. These findings may reflect interspecific differences in the use of this resource, with predatory behavior in Brown Skuas and scavenging behavior in South Polar Skuas (Young 1990; Santos et al. 2012; Golubev 2024). This interpretation is supported by the observation of spontaneous regurgitation events containing penguin remains, which were recorded exclusively in Brown Skua individuals during the study seasons. When excluding feathers as prey item, the interspecific dietary difference becomes more pronounced, suggesting that South Polar Skua rely on penguins to a lesser extent than Brown Skua (Fig. 2, Table S1). Previous studies have suggested that feather consumption may fulfill a non-nutritional role; specifically, aiding in pellet formation and inhibiting gastric parasites, thus proposing scavenging as a potential antiparasitic strategy besides its trophic function (Piersma and Van Eerden 1989). In line with this hypothesis, gastrointestinal parasites have been detected in the pellets of piscivorous seabirds, suggesting that pellet formation could play a role in controlling parasite load (Garbin et al. 2019). This highlights a valuable research direction to explore in skuas, particularly given the higher proportion of fish in the diet of South Polar Skuas, which may increase their exposure to diet-transmitted parasites. Hence, both species may utilize penguins differently: Brown Skuas as a primary energy source, by consuming eggs and chicks in synchrony with the penguin breeding season, and South Polar Skuas primarily through scavenging on dead individuals, potentially to facilitate pellet formation and reduce parasitic load.

A notothenioid fish species, the Antarctic silverfish, and a myctophid species, the Antarctic lanternfish, as well as *Gymnocopelus* sp. were identified in pellets (Table 2). These species have also been recorded in skua diets at other Antarctic locations (Malzof and Quintana 2008; Graña Grilli and Montalti 2012; Ibañez et al. 2022). At this latitude, Antarctic fish availability increases during the austral spring and summer (Kellermann 1986; Hubold and Tomo 1989; Hahn et al. 2008; Caccavo et al. 2018). Based on otolith size, South Polar Skua consumed larger Antarctic lanternfish (in length and mass) than Brown Skua, whereas the size of Antarctic silverfish consumed by both species was similar (Please see attachment). Variations in fish size reflect differences in the developmental stage of the species, with individuals at different stages distributed asymmetrically across the water column (Kellermann 1986; Hubold and Tomo 1989; Greely et al. 1999; Caccavo et al. 2018). Larger and older Antarctic lanternfish are generally found at greater depths. Consequently, South Polar Skua likely need to dive deeper to access these larger individuals, whereas Brown Skua focuses on shallower, inshore waters, where smaller individuals of the same species are more prevalent. (Graña Grilli et al. 2023). In addition, larger fish may be actively selected due to their higher lipid and energy content, which is especially advantageous during chick-rearing periods or in species that undertake long foraging trips, such as the South Polar Skua (Golet et al. 2000).

The consumption of Aves category was higher by South Polar Skua compared to Brown Skua (Table 2 and S1). Storm Petrels were the most common consumed by South Polar Skua, although their remains appeared less frequently in pellets than around nests, suggesting an underestimation of their consumption based on pellet analysis (Malzof and Quintana 2008). South Polar Skua may possibly exhibit specialist foraging behavior on this prey, thus supplementing their energy demands (Baker 2001; Carneiro et al. 2014). Alternatively, as Brown Skua monopolize the penguin colony making them unavailable for other predators, South Polar Skua may take advantage on this prey (Young et al. 1988; Ryan and Moloney 1991; Mougeot et al. 1998; Ryan et al. 2009). In line with this assumption, minor contribution of Invertebrata and Mammalia was observed, which could be used as alternative food resources by South Polar Skua, or the result of secondary ingestion, as is likely the case with the single *Eurythenes gryllus* found in one regurgitate.

Prey availability and competition are extrinsic factors that may influence individual foraging behavior (Ratcliffe et al. 2018; Busdieker et al. 2020). Interspecific competition may constrain the accessibility and the apparent abundance of preferred prey, which can result in intra-seasonal diet variation at individual and population levels (Ratcliffe et al. 2018). In the studied seasons, interspecific differences in the use of trophic resources were observed (Fig. 3 and Table S3). During the chick-rearing stage, both skua species relied more on marine resources; however, throughout both breeding stages, South Polar Skuas tended to consume more marine prey (mainly inshore and offshore fish species) across the three breeding seasons. This is likely due to competitive exclusion by Brown Skua, which are larger and considered to be more aggressive (Pietz 1987). Additionally, our results suggest greater dietary flexibility in Brown Skua by supplementing food obtained on land or coastal/inshore waters with feeding in offshore waters throughout the breeding period (Carneiro et al. 2015; Ibañez et al. 2022; Graña Grilli et al. 2023). This behavior may represent an optimal strategy in Brown Skua to cope with the energy requirements for reproduction. Alternatively, resource accessibility is often influenced by the breeding status of prey (Navarro et al. 2009). In colonial species such as penguins, areas of high prey density represent a potential food source for predators; however, they also impose energetic costs as prey often display effective defense strategies (Halupka and Halupka 1996; Busdieker et al. 2020). Young (1994) reported that skuas generally exhibit low predation success on active penguin nests. However, breeding synchrony with penguins may increase access to eggs and chicks—more vulnerable prey than adults, more defensive individuals. In this context, Brown Skuas initiate incubation earlier (mid-November) than South Polar Skuas (mid-December) (Morales unpubl. data), thereby exploiting a temporal window of higher prey vulnerability (Fig. 1D). In contrast, South Polar Skuas begin breeding when penguin chicks are entering or already in the crèche stage, and thus less accessible, likely requiring greater reliance on alternative food sources (Fig. 1D). Thus, earlier breeding and dietary flexibility in Brown Skuas may represent an adaptive strategy to cope with both declining prey accessibility over the season and inherently low predation success on penguin nests.

Resource abundance is related to the number and type of prey consumed by predators. Nevertheless, intra- and interspecific competition and changes in prey availability force organisms to use alternative resources, which result in changes in the niche width (Terraube and Arroyo 2011). Brown Skua displayed a 1.2 wider Standardized Levin's index than South Polar Skua, with an overlap of 70%, when penguin feathers are excluded. These differences agree with studies in other Antarctic locations with sympatry where a partition of the feeding niche occurs (Malzof and Quintana 2008; Graña Grilli et al. 2011; Graña Grilli and Montalti 2012). Furthermore, considering the breeding stage, the Standardized Levin's index increased for both Skua species from incubation towards the chick-rearing stages, likely reflecting that at this stage of high energy demand skuas increase the consumption of different rich energy prey such as fish to improve breeding fitness and chicks quality (van Donk et al. 2017).

Diet of Skuas based on blood stable isotopes

Blood isotopic composition also suggested interspecific differences in the feeding habits of Brown Skuas and South Polar Skuas when breeding in sympatry. The range of δ^{15}N values in RBCs indicated that Brown Skua consumed prey from various trophic levels (Table 3). However, this could also result from the secondary ingestion of penguin stomach contents, which may distort the apparent prey spectrum and overestimate the diversity of prey actually selected by skuas (Norman et al. 1994; Graña Grilli et al. 2023). The δ^{15}N values, and thus the trophic positions of the consumed prey, were higher and had greater standard deviation in Brown Skua compared to South Polar Skua. This contrasts with previous reports on skuas from Barton Peninsula (South Shetland Islands) where no differences were observed between Skua species (Gal et al. 2021), and are similar to those from Brown Skua at this location (Graña Grilli et al. 2023). In agreement with the results from regurgitated pellets, interspecific differences in RBCs for both δ^{15}N and δ^{13}C and in serum only for δ^{13}C were observed, indicating that both species feed in different areas and on different prey (Table 3). The δ^{13}C values of Brown Skua and South Polar Skua broadly reflect their greater reliance on penguins and inshore and more surface-associated prey, and mesopelagic fish, respectively (Cherel and Hobson 2007; Mills et al. 2025), and are consistent with the prey composition identified in the pellet analysis conducted in the present study. Furthermore, the interspecific differences observed in RBCs δ^{15}N and δ^{13}C may be slightly biased towards the consumption of different prey during the pre-laying period (Carneiro et al. 2016).

Foraging in seabirds can vary between sexes, with males and females exhibiting different foraging behaviors and diet during the breeding period (Forero et al. 2002; Lewis et al. 2002; Navarro et al. 2009). Brown Skua and South Polar Skua show sexual size dimorphism with females being considerably larger and heavier than males (Catry et al. 1999; Phillips et al. 2002). Here, there were no significant sex-related differences in blood isotope values, suggesting that males and females feed on similar trophic levels and habitats at this location (Table 3). Supporting our observations, in Brown Skua populations from Bird Island (South Georgia Islands) during late incubation and early chick-rearing, both sexes show similar foraging behavior and habitat use (Phillips et al. 2007; Carneiro et al. 2016). Furthermore, the stable isotope study in Brown Skua at South Georgia found no evidence for sex-specific foraging preferences during the breeding period (Anderson et al. 2009; Carneiro et al. 2014), nor in the habitat use by breeding South Polar Skua at Svarthamaren, Dronning Maud Land (Busdieker et al. 2020).

Ecological niche theory predicts that in closely related sympatric species breeding in environments with limited resources, partitioning of feeding habitats (spatially and temporally) reduces competition (Schoener 1974; Pianka 1981; Robertson et al. 2014). Moreover, ecological segregation among breeding seabirds can be achieved by the combination of diference in timing of breeding, foraging areas and diet (Phillips et al. 2004; Moreno et al. 2016). Here, Brown Skua exhibited a greater isotopic niche breadth than South Polar Skua (Table 3), indicating that Brown Skua feeds on a wider diversity of prey and uses different habitats, which is supported by the Levin´s Index estimated from pellets (Table S3). Interespecific overlap in SEAb was observed, although it was low, 9.6% in serum and 18.2% in RBC, when comparing species as a whole. However, when analyzing sexes separately, South Polar Skua females showed higher overlap with both male and female Brown Skua (Fig. 3; Table S4). This suggests that during the pre-laying and early incubation stages feeding niche partitioning occurs; however, resources consumed by South Polar Skua females may be shared to a lesser extent by Brown Skua. There is a slight overlap in the timing of incubation and chick-rearing in the study species (Fig. 1D). This breeding allochrony may alleviate the interspecific competition for the most abundant resource (penguins). Our results emphazise dietary segregation between these two species, with Brown Skua and South Polar Skua preferring penguins and marine resources (primarily fish), respectively (Graña Grilli and Montalti 2012, 2015). Thus, understanding the diet of these populations is crucial for assessing the potential implications on generalist seabirds populations under environmental changes (Nussey et al. 2007).

Conclusion

This study investigated the feeding ecology of Brown Skua and South Polar Skua when breeding in sympatry at Potter Peninsula, South Shetland Islands, Antarctica. Interspecific differences in diet and trophic niche partitioning were observed; nevertheless, penguins constituted the main prey for both skua species. Brown Skuas relied more heavily on this terrestrial-breeding prey, whereas South Polar Skuas also made substantial use of marine resources. This pattern is consistent with previous studies on these species (Malzof and Quintana 2008; Grana Grilli and Montalti 2012). Furthermore, Brown Skuas exhibited greater dietary diversity and plasticity than South Polar Skuas throughout the breeding season. Results suggested that when coexisting, skuas are able to adapt their feeding behavior to cope with the energy demands (Ibañez et al. 2022), and to alleviate interspecific competition for similar resource within the same area (Petalas et al. 2021).

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Author contributions All author contributed to the study conception and design. Fieldwork, sample collection, data analysis, manuscript design, writing and edition was performed by **Lara M Morales**, data analysis and manuscript revision was performed by **William F Mills**, sample analysis and draft edition was performed by **Paco Bustamante**, **Rocío Mariano-Jelicich**, Fieldwork, sample collection was conducted by **Diego S Torres**, manuscript supervision and funding **Diego Montalti**, data analysis, manuscript supervision, funding and conception of the origina idea was conducted by **Andrés E Ibañez**. All authors read and approved the final final manuscript.

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Data availability Data will be made available on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests that could have appeared to influence the work reported in this paper.

Ethics approval All applicable international, national and institutional guidelines for sampling, care and experimental use of animals for the study were followed 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 Dirección Nacional del Antártico (permits number 2021-FEAMB-CT-GA-29, 2022-FEAMB-CT-GA-22 and 2023-FEAMB-CT-GA-26). In addition, all protocols conducted in this project 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).

References

Aguirre C (1994) Distribution and abundance of birds at Potter Peninsula, 25 de Mayo (King George) Island, South Shetland Islands, Antarctica. Mar Ornithol 23:23–31

Albarrán KK, Alfonso BC, Fógel J, Rozas Sía MG, Abbeduto ML, Casaux R, Juáres MA (2024) Residues of anthropogenic origin found at Stranger Point/Cabo Funes, 25 de Mayo/King George Island, Antarctica. Polar Biol 47:387–398. https://doi.org/10.1007/s00300-024-03241-0

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. https://doi.org/10.1007/s00300-008-0498-9

Ausems ANMA, Kuepper ND, Archuby D et al (2023) Where have all the petrels gone? Forty years (1978–2020) of wilson's storm petrel (*Oceanites oceanicus*) population dynamics at King George Island (Isla 25 de Mayo, Antarctica) in a changing climate. Polar Biol 46:655–672. https://doi.org/10.1007/s00300-023-03154-4

Baker S, Barbraud C (2001) Foods of the South Polar Skua *Catharacta Maccormicki* at Ardery Island, Windmill Islands, Antarctica. Polar Biol 24:59–61. https://doi.org/10.1007/s003000000163

Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64:1675–1691. https://doi.org/10.1093/icesjms/fsm152

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. https://doi.org/10.1086/342800

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012. https://doi.org/10.1111/j.0021-8790.2004.00861.x

Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28. https://doi.org/10.1086/343878

Bond A, Hobson KA (2012) Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. Waterbirds 35:324–331. https://doi.org/10.1675/063.035.0213

Borghello P, Torres D, Montalti D, Ibañez A (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. https://doi.org/10.1007/s00300-018-2429-8

Burton RW (1968) Agonistic behaviour of the brown skua, *Catharacta skua lonnbergi* (Mathews). Br Antarct Surv Bull 16:15–39

Busdieker KM, Patrick SC, Trevail AM, Descamps S (2020) Prey density affects predator foraging strategy in an Antarctic ecosystem. Ecol Evol 10:350–359. https://doi.org/10.1002/ece3.5899

Caccavo JA, Papetti C, Wetjen M, Knust R, Ashford JR, Zane L (2018) Along-shelf connectivity and circumpolar gene flow in Antarctic silverfish (*Pleuragramma antarctica*). Sci Rep 8:17856. https://doi.org/10.1038/s41598-018-36030-x

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. https://doi.org/10.1007/s00227-014-2457-z

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. https://doi.org/10.1007/s10336-015-1156-y

Carneiro APB, Manica A, Phillips RA (2016) Long-term changes in population size, distribution and productivity of Skuas (*Stercorarius* spp.) at Signy Island, South Orkney Islands. Polar Biol 39:617–625. https://doi.org/10.1007/s00300-015-1817-6

Catry P, Phillips RA, Furness RW (1999) Evolution of reversed sexual size dimorphism Inskuas and jaegers. Auk 116:158–168. https://doi.org/10.2307/4089462

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. Ecol Prog Ser 329:281–287. https://doi.org/10.3354/meps329281

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576. https://doi.org/10.2307/1934144

Coplen TB (2011) Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Commun Mass Spectrom 25:2538–2560. https://doi.org/10.1002/rcm.5129

Daneri GA, Carlini AR, Hernandez CM, Harrington A (2005) The diet of Antarctic fur seals, *Arctocephalus gazella*, at King George Island, during the summer–autumn period (2005) Polar Biol 28:329–333. https://doi.org/10.1007/s00300-004-0693-2

Daneri GA, Carlini AR, Marschoff ER, Harrington A, Negrete J, Mennucci JA, Márquez MEI (2015) The feeding habits of the Southern elephant seal, *Mirounga leonina*, at Isla 25 de Mayo/King George Island, South Shetland Islands. Polar Biol 38:665–676. https://doi.org/10.1007/s00300-014-1629-0

de Brooke M L (2004) The food consumption of the world's seabirds. Proc R Soc Lond B 271:S246–S248. https://doi.org/10.1098/rsbl.2003.0153

Dehnhard N, Achurch H, Clarke J et al (2020) High inter- and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: generalist foraging as an adaptation to a highly variable environment? J Anim Ecol 89:104–119. https://doi.org/10.1111/1365-2656.13078

Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. Colon Waterbirds 9:1. https://doi.org/10.2307/1521138

Emslie S, Karnovsky N, Trivelpiece W (1995) Avian predation at Penguin colonies on King George Island, Antarctica. Wilson Bull 107:317–327

Forero MG, Hobson KA, Bortolotti GR, Donázar JA, Bertelloti M, Blanco G (2002) Food resource utilisation by the Magellanic Penguin evaluated through stable isotope analysis: segregation by sex and age and influence on offspring quality. Mar Ecol Prog Ser 234:289–299. https://doi.org/10.3354/meps234289

Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-Ratite birds. J Avian Biol 30:116. https://doi.org/10.2307/3677252

Furness RW (1987) The Skuas. A.D. Poyser, Calton

Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. ICES J Mar Sci 54:726–737. https://doi.org/10.1006/jmsc.1997.0243

Gal J-K, Choi B, Kim B-K, Jung J-W, Min J-O, Lee WY, Shin K-H, Kim J-H, Ha S-Y (2021) Trophic niche of seabirds on the Barton Peninsula, King George Island, Antarctica. Estuar Coast Shelf Sci 258:107443. https://doi.org/10.1016/j.ecss.2021.107443

Garbin L, Díaz JI, Morgenthaler A, Millones A, Kuba L, Fuchs D, Navone GT (2019) Cormorant pellets as a tool for the knowledge of parasite-intermediate host associations and nematode diversity in the environment. Helminthologia 56:296–302. https://doi.org/10.2478/helm-2019-0027

Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. Auk 117:82–91. https://doi.org/10.1093/auk/117.1.82

Golubev S (2024) Diet and feeding behavior of the South Polar Skuas *Stercorarius maccormicki* in the Haswell Islands, East Antarctica. Birds 5:240–254. https://doi.org/10.3390/birds5020016

Graña Grilli M, Montalti D (2012) Trophic interactions between brown and South Polar skuas at deception Island, Antarctica. Polar Biol 35:299–304. https://doi.org/10.1007/s00300-011-1054-6

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. https://doi.org/10.1007/s00300-014-1627-2

Graña Grilli M, Libertelli M, Montalti D (2011) Diet of South Polar Skua chicks in two areas of sympatry with brown Skua. Waterbirds 34:495–498. https://doi.org/10.1675/063.034.0412

Graña Grilli M, Di Virgilio A, Alarcón P, Cherel Y (2023) Apparent mismatch between stable isotopes and foraging habitat suggests high secondary ingestion of Antarctic krill in brown skuas. Mar Ecol Prog Ser 708:163–176. https://doi.org/10.3354/meps14277

Greely T, Gartner JV Jr, Torres J (1999) Age and growth of *Electrona Antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern ocean. Mar Biol 133:145–158. https://doi.org/10.1007/s002270050453

Hahn S, Peter H-U (2003) Feeding territoriality and the reproductive consequences in brown Skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552–559. https://doi.org/10.1007/s00300-003-0522-z

Hahn S, Peter H-U, Quillfeldt P, Reinhardt K (1998) The birds of the potter Peninsula, King George Island, South Shetland Islands, Antarctica, 1965–1998. Mar Ornithol 26:1–6

Hahn S, Ritz MS, Reinhardt K (2008) Marine foraging and annual fish consumption of a South Polar Skua population in the maritime Antarctic. Polar Biol 31:959–969. https://doi.org/10.1007/s00300-008-0436-x

Halupka K, Halupka L (1996) The influence of reproductive seasonstage on nest defence by meadow Pipits (*Anthus pratensis*). Ethol Ecol Evol 9:89–98. https://doi.org/10.1080/08927014.1997.9522905

Hecht T (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J Antarct Res 71:1–87

Hipfner JM, McFarlane-Tranquilla L, Addison B, Hobson KA (2013) Trophic responses to the hatching of offspring in a central-place foraging seabird. J Ornithol 154:965–970. https://doi.org/10.1007/s10336-013-0962-3

Hobson KA, Clark RG (1993) Turnover of 13 C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. Auk 110:638–641

Hubold G, Tomo AP (1989) Age and growth of Antarctic silverfish *Pleuragramma antarcticum* Boulenger, 1902, from the Southern Weddell sea and Antarctic Peninsula. Polar Biol 9:205–212. https://doi.org/10.1007/BF00263768

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. https://doi.org/10.1007/s00300-021-02993-3

Jackson AL, Parnell AC (2023) SIBER: Stable Isotope Bayesian Ellipses in R. R package version 2.1.7. https://CRAN.Rproject.org/package=SIBER

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable isotope bayesian ellipses in R. J Anim Ecol 80:595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jakubas D, Iliszko LM, Strøm H, Helgason HH, Stempniewicz L (2018) Flexibility of foraging strategies of the great skua *Stercorarius Skua* breeding in the largest colony in the Barents sea region. Front Zool 15:9. https://doi.org/10.1186/s12983-018-0257-x

Kellermann A (1986) Geographical distribution and abundance of postlarval and juvenile *Pleuragramma antarcticum* (Pisces, Notothenioidei) off the Antarctic Peninsula. Polar Biol 6:111–119. https://doi.org/10.1007/BF00258262

Krebs CJ (1999) Ecological Methodology. Benjamin/Cummings, New York

Lanusse L, Sánchez J, Negrete J, Lizarralde M, Poljak S (2022) Elephant seals (*Mirounga leonina*) at potter Peninsula, King George Island, antarctica: genetic variation of the breeding colony and gene flow with other colonies. Polar Biol 45:395–403. https://doi.org/10.1007/s00300-021-02996-0

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, Post DM, Bearhop S (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol Rev 87:545–562. https://doi.org/10.1111/j.1469-185x.2011.00208.x

Levins R (1968) Evolution in changing environments. Princeton University Press, Princeton

Lewis S, Benvenuti S, Dall–Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proc R Soc Lond B Biol Sci 269:1687–1693. https://doi.org/10.1098/rspb.2002.2083

Malzof SL, Quintana RD (2008) Diet of the South Polar Skua *Catharacta Maccormicki* and the brown Skua *C. antarctica lonnbergi* at Cierva Point, Antarctic Peninsula. Polar Biol 31:827–835. https://doi.org/10.1007/s00300-008-0421-4

Matsuoka K, Skoglund A, Roth G et al (2021) Quantarctica, an integrated mapping environment for Antarctica, the Southern Ocean, and sub-Antarctic islands. Environ Model Softw 140:105015. https://doi.org/10.1016/j.envsoft.2021.105015

Mills WF, Ibañez AE, Carneiro APB, Morales LM, Mariano-Jelicich R, McGill RAR, Montalti D, Phillips RA (2024) Migration strategies of Skuas in the Southwest Atlantic ocean revealed by stable isotopes. Mar Biol 171:27. https://doi.org/10.1007/s00227-023-04347-5

Mills WF, Ibañez AE, Bustamante P, Waterman J, Morales LM, Mariano-Jelicich R, Montalti D, Black S (2025) Mercury contamination of sympatric seabirds and associated health risks in an Antarctic ecosystem. Environ Res 281:121990. https://doi.org/10.1016/j.envres.2025.121990

Moreno R, Stowasser G, McGill RAR, Bearhop S, Phillips RA (2016) Assessing the structure and temporal dynamics of seabird communities: the challenge of capturing marine ecosystem complexity. J Anim Ecol 85:199–212. https://doi.org/10.1111/1365-2656.12434

Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown skua (*Catharacta skua lonnbergi*) at Mayes Island, Kerguelen. J Zool 244:429–438. https://doi.org/10.1111/j.1469-7998.1998.tb00047.x

Navarro J, Louzao M, Igual JM et al (2009) Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. Mar Biol 156:2571–2578. https://doi.org/10.1007/s00227-009-1281-3

Norman FI, McFarlane RA, Ward SJ (1994) Carcasses of adelie penguins as a food source for South Polar skuas: some preliminary observations. Wilson Bull 106:26–34

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol 20:831–844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University, Columbus, pp 155–177

Parmelee DF (1988) The hybrid skua: a Southern Ocean enigma. Wilson Bull 100:345–356

Petalas C, Lazarus T, Lavoie RA, Elliott KH, Guigueno MF (2021) Foraging niche partitioning in sympatric seabird populations. Sci Rep 11:2493. https://doi.org/10.1038/s41598-021-81583-z

Peter H-U, Kaiser M, Gebauer A (1990) Ecological and morphological investigations on South Polar Skuas (*Catharacta maccormicki*) and brown Skuas (*Catharacta skua lonnbergi*) on Fildes Peninsula, King George Island, South Shetland Islands. Zool Jb Syst 117:201–218

Phillips RA, Dawson DA, Ross DJ (2002) Mating patterns and reversed size dimorphism in Southern Skuas (*Stercorarius Skua lonnbergi*). Auk 119:858–863. https://doi.org/10.2307/4089989

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. https://doi.org/10.1007/s00300-004-0633-1

Phillips RA, Catry P, Silk JRD, Bearhop S, McGill R, Afanasyev V, Strange IJ (2007) Movements, winter distri-bution and activity patterns of Falkland and brownskuas: insights from loggers and isotopes. Mar Ecol Prog Ser 345:281–291. https://doi.org/10.3354/meps06991

Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Mar Ecol Prog Ser 578:117–150. https://doi.org/10.3354/meps12217

Pianka ER (1981) Competition and niche theory. In: May RM (ed) Theoretical ecology. Blackwell, Oxford, UK, pp 167–196

Piersma T, Eerden MRV (1989) Feather eating in great crested grebes *Podiceps cristatus*: a unique solution to the problems of debris and gastric parasites in fish-eating birds. Ibis 131:477–486. https://doi.org/10.1111/j.1474-919X.1989.tb04784.x

Pietz PJ (1987) Feeding and nesting ecology of sympatric South Polar and brown Skuas. Auk 104:617–627

QGIS.org (2024) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org

R Core Team (2022) R: a Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ratcliffe N, Adlard S, Stowasser G, McGill R (2018) Dietary divergence is associated with increased intra-specific competition in a marine predator. Sci Rep 8:6827. https://doi.org/10.1038/s41598-018-25318-7

Reid A (2016) Cephalopods of Australia and Sub-Antarctic territories. Csiro Publishing

Reinhardt K, Hahn S (2000) A review of the diets of Southern hemisphere Skuas. Mar Ornithol 28:7–19

Reis AO, de Costa A, Torres ES, Alves JPM (2021) MA dos S Pellets and prey remains as indicators of the diet of two sympatric Skuas (aves: Stercorariidae) on King George Island, Antarctica. Oecologia Aust 25:674–684. https://doi.org/10.4257/oeco.2021.2503.04

Ritz MS, Hahn S, Janicke T, Peter H-U (2006) Hybridisation between South Polar Skua (*Catharacta maccormicki*) and brown Skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region. Polar Biol 29:153–159. https://doi.org/10.1007/s00300-005-0034-0

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. https://doi.org/10.1016/j.ympev.2008.07.014

Robertson GS, Bolton M, Grecian WJ, Wilson LJ, Davies W, Monaghan P (2014) Resource partitioning in three congeneric sympatrically breeding seabirds: foraging areas and prey utilization. Auk 131:434–446. https://doi.org/10.1642/AUK-13-243.1

Ryan PG, Moloney CL (1991) Prey selection and temporal variation in the diet of subantarctic Skuas at Inaccessible Island, Tristan Da Cunha. Ostrich 62:52–58

Ryan PG, Whittington PA, Crawford RJM (2009) A tale of two islands: contrasting fortunes for subantarctic Skuas at the Prince Edward Islands. Afr J Mar Sci 31:431–437. https://doi.org/10.2989/AJMS.2009.31.3.16.1004

Sander M, Balbão TC, Polito MJ, Costa ES, Carneiro APB (2007) Recent decrease in chinstrap Penguin (*Pygoscelis antarctica*) populations at two of Admiralty bay's islets on King George Island, South Shetland Islands, Antarctica. Polar Biol 30:659–661. https://doi.org/10.1007/s00300-007-0259-1

Santos MM, Juáres MA, Rombolá EF, García ML, Coria NR, Doncaster CP (2012) Over-representation of bird prey in pellets of South Polar Skuas. J Ornithol 153:979–983. https://doi.org/10.1007/s10336-012-0840-4

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39. https://doi.org/10.1126/science.185.4145.27

Schories D, Kohlberg G (2016) Marine Wildlife, King George Island, Antarctica. Dirk Schories

Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct Ecol 17:66–74. https://doi.org/10.1046/j.1365-2435.2003.00705.x

Terraube J, Arroyo B (2011) Factors influencing diet variation in ageneralist predator across its range distribution. Biodivers Conserv 20:2111–2131. https://doi.org/10.1007/s10531-011-0077-1

Trillmich F (1978) Feeding territories and breeding success of South Polar Skuas. Auk 95:23–33. https://doi.org/10.2307/4085492

Trivelpiece W, Volkman NJ (1982) Feeding strategies of sympatric South Polar *Catharacta maccormicki* and brown skuas *C. lönnbergi*. Ibis 124:50–54. https://doi.org/10.1111/j.1474-919X.1982.tb03740.x

Trivelpiece W, Butler RG, Volkman NJ (1980) Feeding territories of brown skuas (*Catharacta lonnbergi*). Auk 97:669–676

van Donk S, Camphuysen KCJ, Shamoun-Baranes J, van der Meer J (2017) The most common diet results in low reproduction in ageneralist seabird. Ecol Evol 7:4620–4629. https://doi.org/10.1002/ece3.3018

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10:e0116182. https://doi.org/10.1371/journal.pone.0116182

Velarde E, Anderson DW, Ezcurra E (2019) Seabird clues to ecosystem health. Science 365:116–117. https://doi.org/10.1126/science.aaw9999

Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. Polar Biol 26:20–26. https://doi.org/10.1007/s00300-002-0446-z

Votier SC, Bearhop S, Ratcliffe N, Furness RW (2004) Reproductive consequences for great skuas specializing as seabird predators. Condor 106:275–287. https://doi.org/10.1093/condor/106.2.275

Votier SC, Bearhop S, Crane JE, Arcos JM, Furness RW (2007) Seabird predation by great Skuas *stercorarius* skua -intra-specific competition for food? J Avian Biol 38:234–246. https://doi.org/10.1111/j.0908-8857.2007.03893.x

Xavier JC, Cherel Y (2009) Cephalopod beak guide for the Southern ocean. British Antarctic Survey, Cambridge, UK

Xavier JC, Cherel Y, Boxshall GA et al (2020) Crustacean guide for predator studies in the Southern ocean. Scientific Committee on Antarctic Research, Cambridge, UK

Young EC (1990) Diet of the South Polar Skua determined from regurgitated pellets: limitation of a technique. Polar Rec 26:124–125

Young EC (1994) Skua and penguin: predator and prey. Cambridge, New York

Young EC, Jenkins PE, Douglas ME, Lovegrove TG (1988) Nocturnal foraging by Chatham Island Skuas. NZ J Ecol 11:113–117

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