Apparent mismatch between stable isotopes and foraging habitat suggests high secondary ingestion of Antarctic krill in brown skuas

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ABSTRACT: Changes in seasonal resource availability and in energetic requirements as offspring grow may force parents to change their trophic ecology throughout the breeding season. Brown skuas *Stercorarius antarcticus* breed in a highly seasonal environment where the availability of their main food resource changes during the season. We studied the feeding plasticity of breeding brown skuas by assessing their isotopic diet and movement patterns at different stages of their breeding cycle. Blood $\delta^{15}N$ values indicated that penguin chicks *Pygoscelis* spp. and Antarctic krill *Euphausia superba* constituted most of the diet of brown skuas (up to ~70%), and that there was an increase in the ingestion of lower trophic level prey (most likely Antarctic krill) throughout the breeding period (from 30–46%). This contrasts with movement analysis indicating that 65% of the overall foraging locations were within penguin rookeries. The apparent contradiction between the results from both techniques may be explained by a combination of some skuas feeding mostly at sea or on shore together with secondary ingestion of marine resources from the penguins' gut by feeding mostly within penguin rookeries. Krill obtained in that way may provide protein to replenish reserves before migration along with globulins through the intake of carotenoids. These results highlight the fact that the trophic ecology of species can be more complex than that suggested by one single method and emphasizes the importance of combining techniques to draw robust conclusions. In addition, our study indicates that skuas may select portions of prey to obtain specific resources to fulfill their nutritional requirements.

KEY WORDS: Antarctica · Isotopic analysis · Movement · South Shetland Islands · *Stercorarius antarcticus* · Trophic ecology

1. INTRODUCTION

Predators and scavengers inhabiting polar environments face changes in the availability of food resources throughout their breeding period (i.e. spring and summer). Moreover as the offspring develops, parental care decreases, and its energetic demands increase (Weimerskirch et al. 2000, Weimerskirch & Lys 2000, Hahn et al. 2007), causing a change in the parents' feeding frequency, location, and/or resources selected (Bradley et al. 2004, Bujoczek & Ciach 2009, Markones et al. 2010). Feeding plasticity allows a species to take advantage of varying resources and, therefore, to deal with changes in food availability and demand (Hamer et al. 2007, Carneiro et al. 2015, Booth et al. 2018). This flexibility may also confer the species the ability to adapt to environmental changes that modify food resources over long time scales, to reduce competition, and to meet physiological needs (Wakefield et al. 2013, Robertson et al. 2014, Negrete et al. 2017, Booth et al. 2018).

Brown skuas *Stercorarius antarcticus* have an opportunistic diet, preying or scavenging on many species of birds, fish, marine invertebrates, and mammals,

including domestic ones (Peter et al. 1990, Moncorps et al. 1998, Reinhardt et al. 2000, Schultz et al. 2021, Travers et al. 2021). In many areas, skua nesting sites are strongly associated with penguin rookeries, where they mostly feed on penguin eggs and chicks (Burton 1968, Pietz 1987). The availability of these penguin items changes during the breeding period of brown skuas: high availability of eggs is followed by the appearance and predominance of chicks, which become less vulnerable to being preyed upon by skuas as they grow up. Penguin rookeries offer almost nothing but carcasses as food at the end of the brown skuas' breeding season (Müller-Schwarze & Müller-Schwarze 1973, Young 2005). At Potter Peninsula, King George Island, brown skuas are strongly associated with a mixed penguin colony of Adélie and gentoo penguins, which constitutes their main food resource (Hahn et al. 2005, Hahn & Bauer 2008). In contrast, the biomass density of Antarctic krill remains constant throughout the season but their demography changes, showing an increase in the proportion of individuals with larger body size (Hewitt et al. 2004). The abundance at sea of pelagic fish decreases from September to October and then recovers in March (Casaux et al. 1990). Due to their opportunistic feeding habits and the seasonal change in feeding resources, brown skuas are likely to show dietary plasticity in self-feeding in response to those changes in resource availability and the energetic requirements of their offspring (Carneiro et al. 2015, Graña Grilli & Montalti 2015).

Many techniques are used to study the diet of seabirds, including the traditional methods of stomach content analysis (Wilson 1984, Colabuono & Vooren 2007), visual observation (Ostrand et al. 1998, Aygen & Emslie 2006), and pellet and feces analyses (Moncorps et al. 1998, Kubetzki et al. 1999, Santos et al. 2012, Pacoureau et al. 2019, Ibañez et al. 2022). These methods provide information on ingested items but have some limitations because it can be difficult to identify prey items during observed feeding events and the variation in the relative importance of items according to their different digestibility when analyzing pellets (Santos et al. 2012). Stable isotope analyses indicate the integrated isotopic value of dietary items that have been absorbed (Hobson & Clark 1992a). However, all potential prey available in the environment as well as the turnover rate of the analyzed tissues must be considered in order to draw appropriate conclusions (Bond & Jones 2009). Results can be difficult to interpret, but they can be related to the isotopic value of the prey items present in the environment to estimate the composition of the diet

(Hobson et al. 1994, Bearhop et al. 2004). Individual movements provide complementary information by pointing to potential food resources within the foraging range of individual animals (Elliott et al. 2008), although their presence at any site does not guarantee that specific resources are taken from these locations (Johnson 1980). No single method provides complete data on a species' diet; therefore, the use of a combination of techniques may help to obtain a more complete picture of a species' trophic ecology.

We aimed to assess the feeding plasticity of brown skuas by studying changes in their self-feeding habits throughout the breeding season by combining the analysis of stable isotopes (δ^{13}C and δ^{15}N) of blood with GPS tracking data, which allowed us to assess the composition of the skuas' assimilated food and feeding sites, respectively. Due to the strong relationship of brown skua nesting sites with penguin rookeries as a food resource, the *a priori* expectation was that both the isotopic values and the GPS locations would indicate high use of penguin rookeries throughout the breeding period. In addition, we expected to observe a gradual increase in the use of krill and fish (hereafter, marine resources) towards the end of the breeding period to compensate for the decrease in the availability of resources from the penguin rookeries as penguin chicks grow and are less vulnerable prey, coinciding with the increased energetic demands of the skua chicks.

2. MATERIALS AND METHODS

2.1. Study area and sampling

The study was carried out on the Potter Peninsula, King George Island, Antarctica (62° 15' S, 58° 40' W) during the brown skua incubation and chick-rearing periods (mid-November through January) of austral summers 2012–2013 and 2013–2014. The study site had a mixed colony of approximately 8700 pairs of Adélie *Pygoscelis adeliae* and gentoo *P. papua* penguins (Juáres et al. 2016) (see Fig. 1). The laying peak of Adélie penguins is around mid-November (Carlini et al. 2009), and that of gentoo penguins in late-November in years with high snow accumulation (as it was during the 2013–2014 season when most of our sampling was carried out) (Juáres et al. 2013). Penguin chicks hatch around 37 d after laying and crèche at around 25 d old (García-Borboroglu & Boersma 2015). The average distance from a skua nest to the nearest penguin rookery was 79 m (range: 12–179 m); no skua nest was located inside a rookery.

Using a net-gun, we captured both members of 11 breeding pairs of brown skuas at 3 stages of their breeding period: (1) incubation, (2) early chick-rearing, and (3) late chick-rearing. Deployment of GPS units was done as soon as the egg was discovered, the chick hatched, or the chick developed cover feathers for the incubation, early chick-rearing, or late chick-rearing stages, respectively. During these captures, we equipped each bird with a GPS device (CatTrack GPS logger, Perthold Engineering; weight: 20 g; mean ± SD female weight: 1.85 ± 0.13 kg; male weight: 1.73 ± 0.11 kg; 1.2% of male body weight), attached with tape to the back feathers between the wings (Wilson et al. 1997), and set to record locations every 10 min. Approximately 10 d after deployment, birds were re-captured to recover the GPS units and to collect blood samples for dietary stable isotope analysis. Blood samples were separated into plasma and red blood cells (RBCs) by centrifuging; each sample was stored frozen. During fieldwork, we sampled all actively breeding pairs at Potter Peninsula. Once pairs failed a breeding attempt, we were not able to recapture them. Due to frequent and unforeseen breeding failures during incubation and chick-rearing (Graña Grilli 2014), sample sizes are unbalanced between stages (Table 1).

Table 1. Brown skuas *Stercorarius antarcticus* sampled at Potter Peninsula, King George Island, during the 2013–2014 breeding season. Samples taken in the previous season are specified. Bird ID, pairs (same nest number), sex (M: male; F: female; NA: not available), breeding stage (incubation, early or late rearing) capture/recapture date, weight, foraging strategy (penguin rookery, at sea, shore area) and C and N stable isotopes from red blood cells for each bird are detailed. (–) No data available; (*) birds used in the stable isotope mixing model

ID	Nest	Sex	Stage	Capture/ recapture date	Weight at capture (kg)	% Penguin feeding	% Sea feeding	% Shore feeding	Red blood cells $\delta^{13}C$	$\delta^{15}N$
MBM*	1	F	Incubation	29 Nov/9 Dec	1.80	97.0	2.9	0.0	−22.4	11.9
			Early rearing	2 Jan/11 Jan	1.96	96.8	3.2	0.0	−24.4	11.2
			Late rearing	29 Jan/10 Feb	1.72	98.5	0.8	0.7	−25.1	10.1
MJL*	1	M	Incubation	29 Nov/9 Dec	1.62	96.4	3.4	0.2	−22.5	11.9
			Early rearing	2 Jan/11 Jan	1.60	99.2	0.8	0.0	−24.7	11.1
			Late rearing	29 Jan/10 Feb	1.52	95.9	3.5	0.6	−25.1	9.7
MBP*	2	F	Incubation	5 Dec/15 Dec	1.69	98.9	1.1	0.0	−23.8	11.0
			Early rearing	2 Jan/11 Jan	1.82	97.2	1.1	1.7	−24.9	10.4
MKE*	2	M	Incubation	5 Dec/15 Dec	1.75	100.0	0.0	0.0	−23.8	11.8
			Early rearing	2 Jan/15 Jan	1.68	97.0	3.0	0.0	−25.4	10.6
MIY*	3	F	Early rearing	30 Dec/8 Jan	2.00	34.0	45.8	20.2	−24.9	10.7
			Late rearing	13 Feb/22 Feb	1.88	25.2	61.3	13.5	−	−
MHZ*	3	M	Incubation	5 Dec/16 Dec	1.90	38.3	43.5	18.1	−23.7	12.1
			Early rearing	30 Dec/8 Jan	1.60	30.9	51.3	17.9	−24.5	11.2
MAR	4	F	Incubation	23 Nov/2 Dec	1.90	89.0	8.0	2.9	−23.3	11.8
A89	4	M	Incubation	23 Nov/2 Dec	1.77	70.5	23.6	6.0	−22.9	11.8
MSR	5	F	Incubation	29 Nov/9 Dec	1.95	11.8	57.1	31.1	−23.0	12.2
A61	5	M	Incubation	29 Nov/9 Dec	1.78	17.4	49.2	33.3	−23.2	12.5
MBE	6	F	Incubation	24 Nov/5 Dec	1.79	94.1	5.4	0.4	−23.5	10.9
MBA	6	M	Incubation	22 Nov/5 Dec	1.70	98.1	1.8	0.0	−21.7	13.5
MCM	7	F	Incubation	22 Nov/2 Dec	1.88	4.5	90.9	4.5	−22.4	10.7
MBL	7	M	Incubation	23 Nov/2 Dec	1.72	100.0	0.0	0.0	−23.0	12.3
MBS	8	F	Incubation	29 Nov/9 Dec	1.96	7.6	86.9	5.5	−23.1	11.6
PN7	8	M	Incubation	29 Nov/9 Dec	1.71	23.8	72.2	4.0	−23.4	11.8
MKJ	9	F	Incubation	16 Dec/23 Dec	1.94	11.6	73.0	14.5	−24.3	10.7
MBY	10	–	Incubation	30 Dec/2 Jan	1.65	0.6	76.6	22.8	−	−
MBA*	11	M	Late rearing	1 Feb/5 Feb (2012−2013)	1.88	94.3	5.7	0.0	−25.4	10.2
MBE*	11	F	Late rearing	1 Feb/11 Feb (2012−2013)	1.95	95.7	4.3	0.0	−25.7	9.3
MAR*	12	F	Late rearing	1 Feb/11 Feb (2012−2013)	1.87	66.7	28.1	5.1	−24.9	10.1
A89*	12	M	Late rearing	1 Feb/11 Feb (2012−2013)	1.65	−	−	−	−24.96	10.1

2.2. Movement analysis

We manually inspected movement data based on distance and speed between consecutive locations and did not find any erroneous locations to remove. To evaluate if the respective importance of different foraging areas changed throughout the breeding season, we modeled the probability that an individual would visit these sites during the 3 studied breeding stages. Based on spatial matching carried out with QGis v.3.26.3, we first classified the GPS locations as belonging to 4 categories: (1) at sea (locations overlapping the sea), (2) penguin rookery (locations overlapping penguin rookeries), (3) shore (a buffer area 5 m each side of the shoreline, where skuas can scavenge on krill and fish in low tide as well as on elephant seal remains, and to account for errors in the mapped shoreline), and (4) other. Data under the category 'other' were excluded from foraging analysis, as these data points included non-foraging areas in or close to the nest or in non-breeder groups with no potential sources of food. We used foraging location as a 3-category response variable in a hierarchical multinomial logistic regression model. In this model, the probability of each foraging location was a function of breeding stage as the predictor. To constrain the probabilities between 0 and 1, we used the multinomial equivalent of a logit link function. In order to capture the hierarchical structure of the data (i.e. GPS locations nested in individual skuas), we constructed a hierarchical model where the individual-level parameters were assumed to be drawn from a common parameter distribution. We implemented the model in JAGS v.4.12 via the package 'jagsUI' v.4.12 for R v.4.2.0 using Bayesian inference (Plummer 2003, R Core Team 2014). Non-informative priors were set to a normal distribution with a mean of 0 and variance of 10 000. We ran 3 chains with 10 000 iterations, discarding the first 5000 as a burn-in. Convergence was evaluated through visual inspection of trace plots and the Gelman-Rubin statistic (Kruschke 2014).

2.3. Stable isotope analysis

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used as proxies of the foraging habitat and diet/trophic level, respectively (Hobson et al. 1994, Bearhop et al. 2002, Jaeger et al. 2010). Stable isotope analysis enables the study of dietary changes in self-feeding over time through repeated and minimally invasive sampling (Hobson & Clark 1992a). As the characteristic metabolic rate of different tissues determines their turnover rate, each one reflects the isotopic composition of the diet during different periods (Hobson & Clark 1992b, Wolf et al. 2009). Despite some variation among species, the half-life time of $\delta^{13}C$ in RBCs (20 d) is much longer than in plasma (3 d), meaning that the isotopic composition of RBCs and plasma integrates isotopes from the diet during a period of ~2 mo vs. 1 wk, respectively (Hobson & Clark 1993). This difference in feeding period integrated by the 2 components of the blood allows the identification of temporal changes in diet (Hobson & Clark 1992b, Wolf et al. 2009).

Values of $\delta^{15}N$ and $\delta^{13}C$ were determined for 17 breeding brown skuas during the 2013–2014 season and 4 skuas during the 2012–2013 season (Table 1 shows sample sizes per breeding stage). Blood samples from the 2013–2014 season were analyzed as RBCs (n = 28) and plasma (n = 20) separately, while those of the 2012–2013 season were analyzed as whole blood, the results of which are comparable to those of RBCs (Cherel et al. 2005a) and belong only to the late chick-rearing stage. These 4 samples were used to complement the samples of RBCs belonging to the late chick-rearing stage of the following season because that stage often had the lowest sample size due to breeding failure (Graña Grilli 2014). The similar isotopic values and C:N mass ratio of RBCs and whole blood make it possible to analyze both kinds of samples pooled (Cherel et al. 2005a).

RBCs and plasma samples were dried to constant weight in a stove at 58°C for 54 h. Since plasma, unlike whole blood and RBCs, contains a high and variable lipid content that affects its $\delta^{13}C$ values (Cherel et al. 2005a,b), lipids were extracted from plasma samples using a solution of chloroform/methanol (Cherel et al. 2005b). Samples were then centrifuged and dried again to constant weight in a stove at 50°C. Once dried, both RBCs and delipidated plasma were powdered with mortar, and a subsample of 0.2–0.5 mg was packed into tin containers. Isotopic measurements were performed using a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Thermo Scientific Flash EA 1112). Results are presented in δ notation (in ‰) relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Using linear mixed-effects models from the R package 'nlme' v.3.1-160 (Pinheiro et al. 2020), we evaluated changes in isotopic values between the 3 stages of the breeding period, also considering the interac-

tion between the stage and the sex of the bird, and used the identity of the birds as a random factor in the intercept. The C:N mass ratio was analyzed in the same way to control for changes in the presence of lipids that could alter the δ^{13}C values (Cherel et al. 2005b).

We also performed a Bayesian stable isotope mixing model using the R package 'SIMMR' v.0.4.5 in order to estimate the composition of the diet of brown skuas during the breeding period (Parnell 2021). This model allowed us to consider the different potential food items and their isotopic discrimination factors (Parnell et al. 2013). The isotopic discrimination factor we used was that of whole blood of great skuas *Stercorarius skua*, a species with a close phylogenetic relationship to brown skuas (Bearhop et al. 2002). The isotopic value of whole blood is comparable to that of RBCs but not to plasma (Cherel et al. 2005a); therefore, we only considered for this analysis the RBC samples of brown skuas. We applied the enrichment factors to the different items according to their similarity with those sources available. We used the enrichment factor and SD based on a piscivorous diet (Δ^{13}C: 1.1 ± 0.9; Δ^{15}N: 2.8 ± 0.7) for krill and fish, and that based on a beef diet (Δ^{13}C: 2.3 ± 1.0; Δ^{15}N: 4.2 ± 0.3) for penguin and elephant seal *Mirounga leonina* items (Bearhop et al. 2002). In addition, we only included samples belonging to the early rearing and late rearing stages (Table 1). This is because if we consider the shorter time elapsed since migration at the incubation stage and the turnover rate of RBC samples, there is a high probability of capturing isotopic remains of the diet from wintering sites and migration in the incubation stage samples.

Selection of food items for inclusion in the model was determined from observations of feeding brown skuas as well as remains found in pellets or around the nests. As a result, the potential items considered were Adélie and gentoo penguin chicks and eggs, adults and pups of elephant seals (whose birth period is finished by the start of the skuas' laying period), fish, and Antarctic krill. Other bird species present in the study site were not included due to their low abundance or because the foraging zone of brown skuas during the study period did not include their nesting sites (M. Graña Grilli pers. obs.).

The isotopic values of penguin chicks were obtained through analysis of blood samples from 10 Adélie and 10 gentoo penguin chicks. Half of the samples of both species belonged to chicks in the brooding stage and the other half belonged to chicks in the crèche stage. Plasma and RBC samples of penguins were obtained and processed in the same way as those from brown skuas. We did not find published isotopic values for penguin egg content measured after lipid extraction; therefore, we used published values for the eggshell membrane of gentoo penguins (Polito et al. 2009), which has a lower initial C:N ratio and is close to that of egg content after lipid extraction (Elliott & Elliott 2016, Calizza et al. 2021). We also used published values of δ^{13}C and δ^{15}N for whole body without carapace of Antarctic krill (Kokubun et al. 2015), Antarctic lanternfish *Electrona antarctica* (Polito et al. 2011), and RBCs of elephant seals (Hückstädt et al. 2012). The isotopic values of elephant seal pups were calculated by correcting the isotopic values of adults and considering the difference in isotopic values between pups and their mothers (Ducatez et al. 2008) (Table 2). We represented fish using the isotopic values of Antarctic lanternfish, the fish species most frequent in the diet of brown skuas at South Shetland Islands (Graña Grilli & Montalti 2012).

Table 2. Isotopic values of prey considered in the stable isotope mixing model for the diet of brown skuas *Stercorarius antarcticus* in Potter Peninsula, King George Island. Values are mean ± SD. Locality and season of collection of samples for isotopic values of reference are indicated

	δ^{13}C	δ^{15}N	N	Locality, season	Reference
Penguin chick (*Pygoscelis adeliae*, *P. papua*)	−27.5 ± 0.3	7.5 ± 0.2	20	King George Island, 2012−2014	This study
Gentoo penguin eggshell membrane	−22.4 ± 1.0	10.5 ± 0.4	20	Livingston Island, 2006	Polito et al. (2009)
Antarctic krill *Euphausia superba*	−27.4 ± 0.5	3.8 ± 0.3	5	King George Island, 2009−2010	Kokubun et al. (2015)
Antarctic lanternfish *Electrona antarctica*	−25.5 ± 0.7	8.8 ± 0.7	41	South Shetland Islands, 2005−2009	Polito et al. (2011)
Elephant seal *Mirounga leonina* adult	−23.2 ± 0.2	10.5 ± 0.2	15	Livingston Island, 2009	Hückstädt et al. (2012)
Elephant seal *M. leonina* pup	−22.9 ± 0.7	11.8 ± 0.4	17	Livingston Island, 2009 Kerguelen Islands, 2006	Ducatez et al. (2008), Hückstädt et al. (2012)

2.4. Effect of space use on the diet

To identify the influence of the relative use of penguin rookeries as foraging habitat, we used correlation analysis to compare the proportion of time skuas spent at penguin rookeries (i.e. feeding on penguins) and the $\delta^{15}N$ value of the plasma samples. Since $\delta^{15}N$ shows an increase of 3–4‰ between trophic levels (Hobson & Welch 1992), we expected a positive correlation with higher $\delta^{15}N$ values when the use of penguin rookeries was higher.

3. RESULTS

3.1. Movement analysis

We deployed 35 GPS units with 69% recovery success. The average (±SD) deployment time was 9.7 ± 1.8 d, from which we obtained an average of 1313 ± 272 locations per bird and per deployment (breeding stage).

GPS data indicated that the proportion of total locations classified within foraging areas (sea, shore, and penguin rookeries together) was (mean ± SD) 0.19 ± 0.10 during incubation, 0.21 ± 0.08 during early rearing, and 0.45 ± 0.15 during the late-rearing stage (Table 1). The 7 skuas that used sea and shore habitat (70%) primarily foraged at sea (Fig. 1). Birds that primarily used penguin rookeries as feeding areas also made trips to the sea, increasing the distance traveled from the nest towards the late-rearing stage (Fig. 2). Overall, skuas used penguin rookeries more than sea and shore habitat throughout the breeding season (multinomial regression probability >0.5; see median values in Fig. 3). However, when we examined this behaviour at the individual level, there was a strong dichotomy: some birds fed mostly within penguin rookeries and others foraged mostly at sea and on shore areas (Fig. 3).

3.2. Stable isotope analysis

The similar C:N mass ratio showed no changes in the lipid content of both RBCs ($F_{2,25} = 0.63$, p = 0.5) and delipidated plasma ($F_{2,17} = 0.37$, p = 0.7) during the breeding period (Table 3), validating the isotopic comparison made between the different breeding stages. The decrease in $\delta^{15}N$ in both tissues indicated an increase in the ingestion of lower trophic level food throughout the breeding period regardless of the predominant feeding area of the birds (Table 3).

The same decreasing trend occurred for $\delta^{13}C$ in RBCs, approaching through time the characteristic low isotopic value of the Antarctic region (Table 3) (Jaeger et al. 2010).

The Bayesian stable isotope mixing model indicated that isotopic values of brown skuas during early and late chick-rearing were close to those of penguin chicks and fish (Fig. 4). The model indicated that at Potter Peninsula, penguin chicks and Antarctic krill constitute most of the diet of brown skuas, and there is a change in the composition of their diet during chick-rearing. Skua diets included more penguin chicks during the early chick-rearing stage and more krill during the late chick-rearing stage (Table 4). It is worth mentioning that, as most of the birds feeding mainly at sea and on shore failed their breeding attempt during incubation, and we did not include samples from the incubation stage in the stable isotope mixing model, this analysis is biased towards birds feeding mainly in penguin rookeries.

Even though movement patterns during incubation showed the use of multiple foraging areas, isotope values for birds feeding mainly within penguin rookeries and at sea/shore showed similar results in plasma ($\delta^{13}C$: $t = 0.7$, p = 0.5; $\delta^{15}N$: $t = 1.2$, p = 0.26) and RBCs ($\delta^{13}C$: $t = 1.0$, p = 0.35; $\delta^{15}N$: $t = 1.0$, p = 0.32).

3.3. Effect of use of space on the diet

The proportional use of penguin rookeries vs. sea and shore was not correlated with plasma $\delta^{15}N$ values (r = −0.31, p = 0.19). Importantly, penguins mainly using penguin rookeries showed a broad scope of $\delta^{15}N$ values, indicating the use of prey items from different trophic levels (Fig. 5).

4. DISCUSSION

Our study shows an apparent mismatch between the relative importance of different food resources used by brown skuas and the foraging areas they visit. As with previous findings, most of the studied birds foraged mainly on penguins (Hahn & Bauer 2008, Graña Grilli & Montalti 2012) and spent most of their time within the penguin rookeries; however, despite this behaviour, their isotopic values indicated ingestion of high amounts of Antarctic krill. In line with our prediction, at the population level, tracking data suggest that many of the studied brown skuas forage in penguin rookeries at a greater proportion than at sea throughout the breeding season. How-
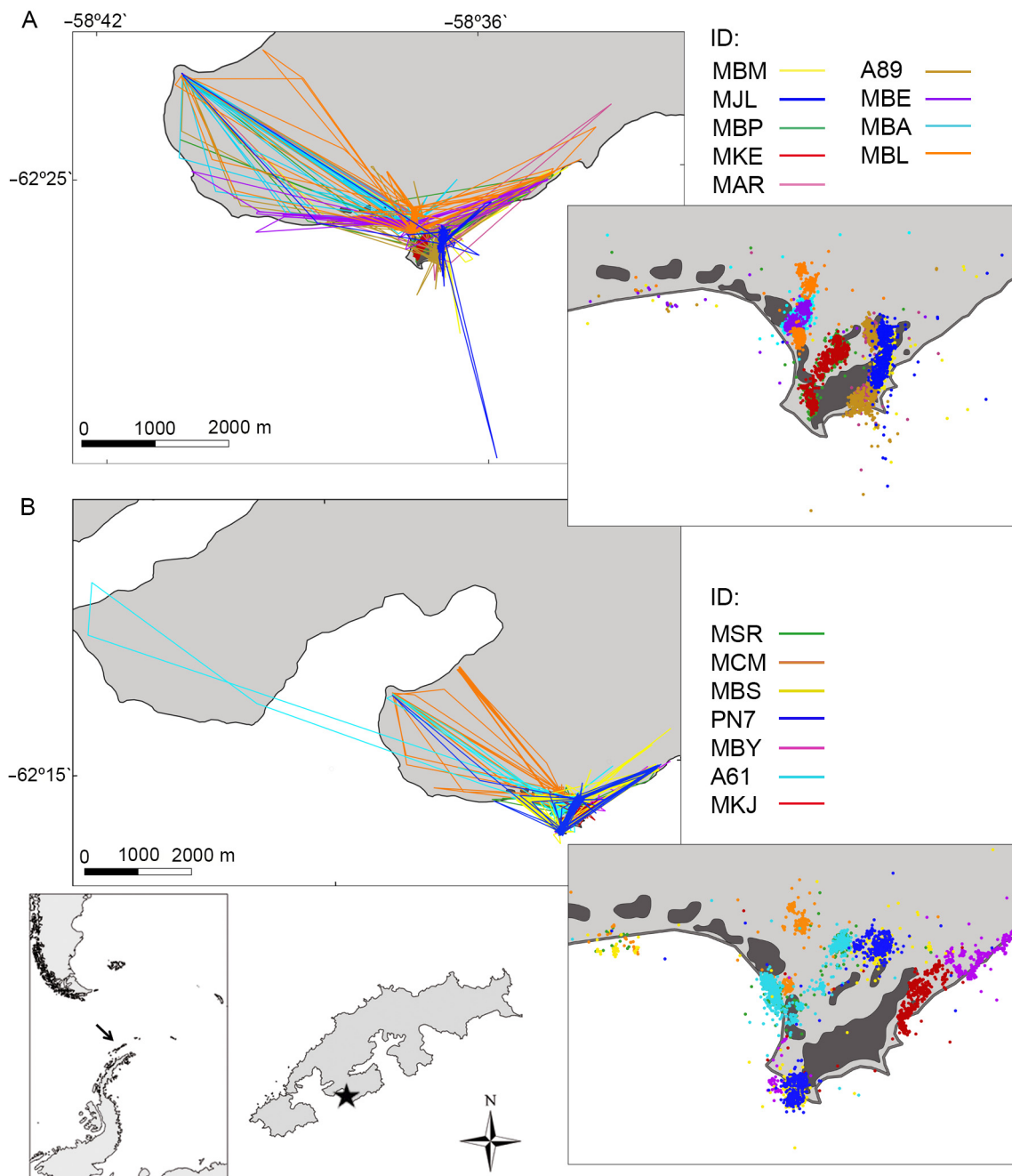
Fig. 1. Movements of (A) 9 brown skuas *Stercorarius antarcticus* foraging >70% on penguin rookeries and (B) 7 brown skuas foraging >70% at sea/shore during the incubation period. Different colors refer to different birds (see Table 1 for details); penguin rookeries are mapped in darker grey

ever, this was not true for all the studied birds, as some of them mostly used the sea and shore as foraging areas. In addition, the low $\delta^{15}N$ values indicated feeding from low trophic level prey, meaning higher use of resources obtained from the sea than expected during the whole breeding period—including fish, despite its low availability during the skuas' breed-

ing season (Casaux et al. 1990). Both the $\delta^{15}N$ values and the Bayesian isotopic mixing model indicated an increase in the ingestion of marine resources (krill and fish) during the breeding period in the studied brown skuas. Such change was not seen in movements; in contrast, there was strong inter-individual variation, with a group of birds consistently using the
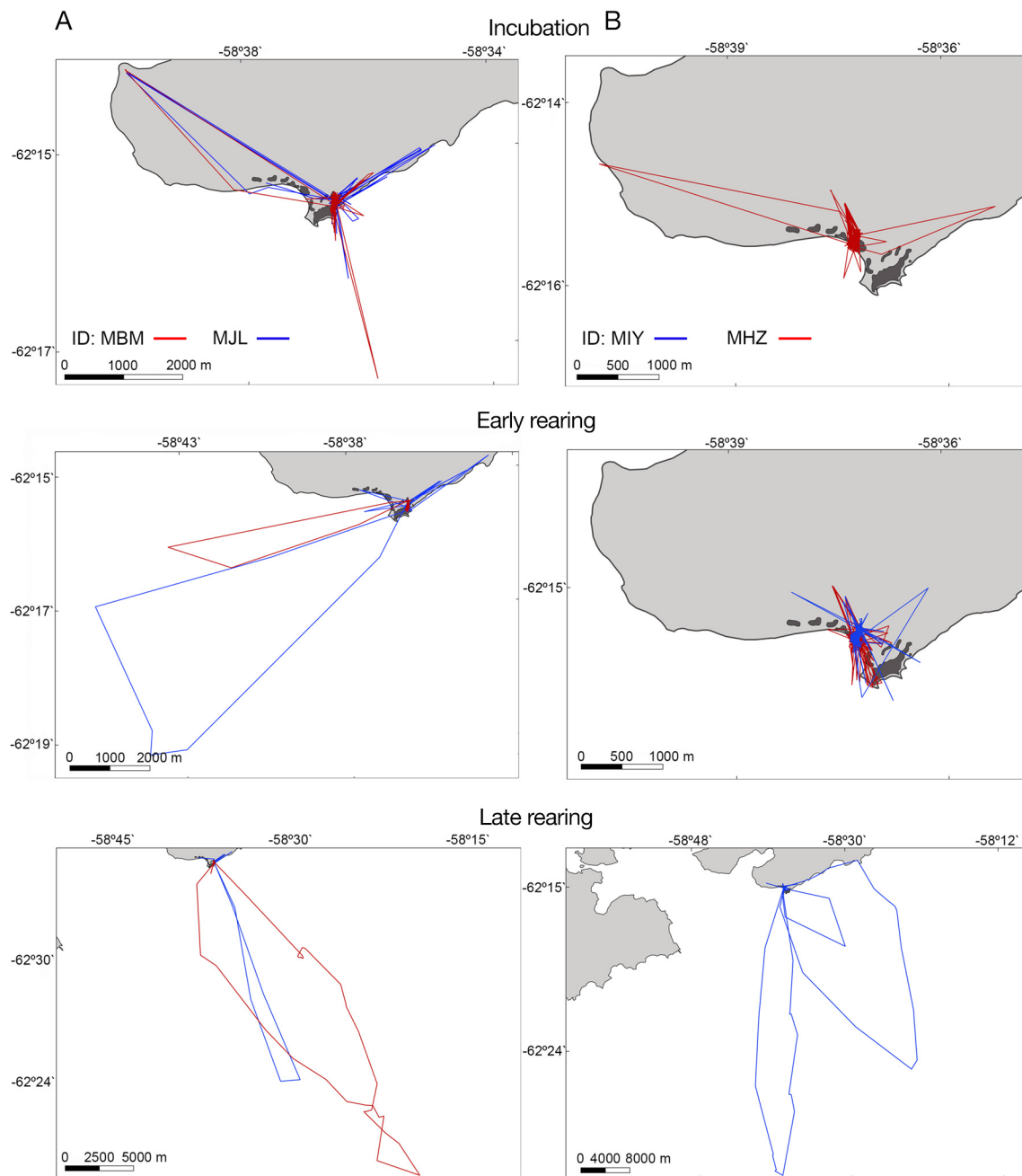
Fig. 2. Change in the movement of both members of a pair of brown skuas *Stercorarius antarcticus* feeding mostly (A) on penguin rookeries and (B) at sea/on shore through the different stages of the breeding period at Potter Peninsula, King George Island

penguin rookeries and another group spending a much higher proportion of time at sea, without intra-individual variation in the predominantly used resource thoughout the season. The Bayesian isotopic mixing model also indicated a considerable proportion of elephant seal and penguin eggs in the diet that decreased towards the later stage of the

brown skuas' breeding period; this may be related to the time of their availability, with Adélie and gentoo penguin egg hatching in late December to early January and elephant seal pups departing to sea in November.

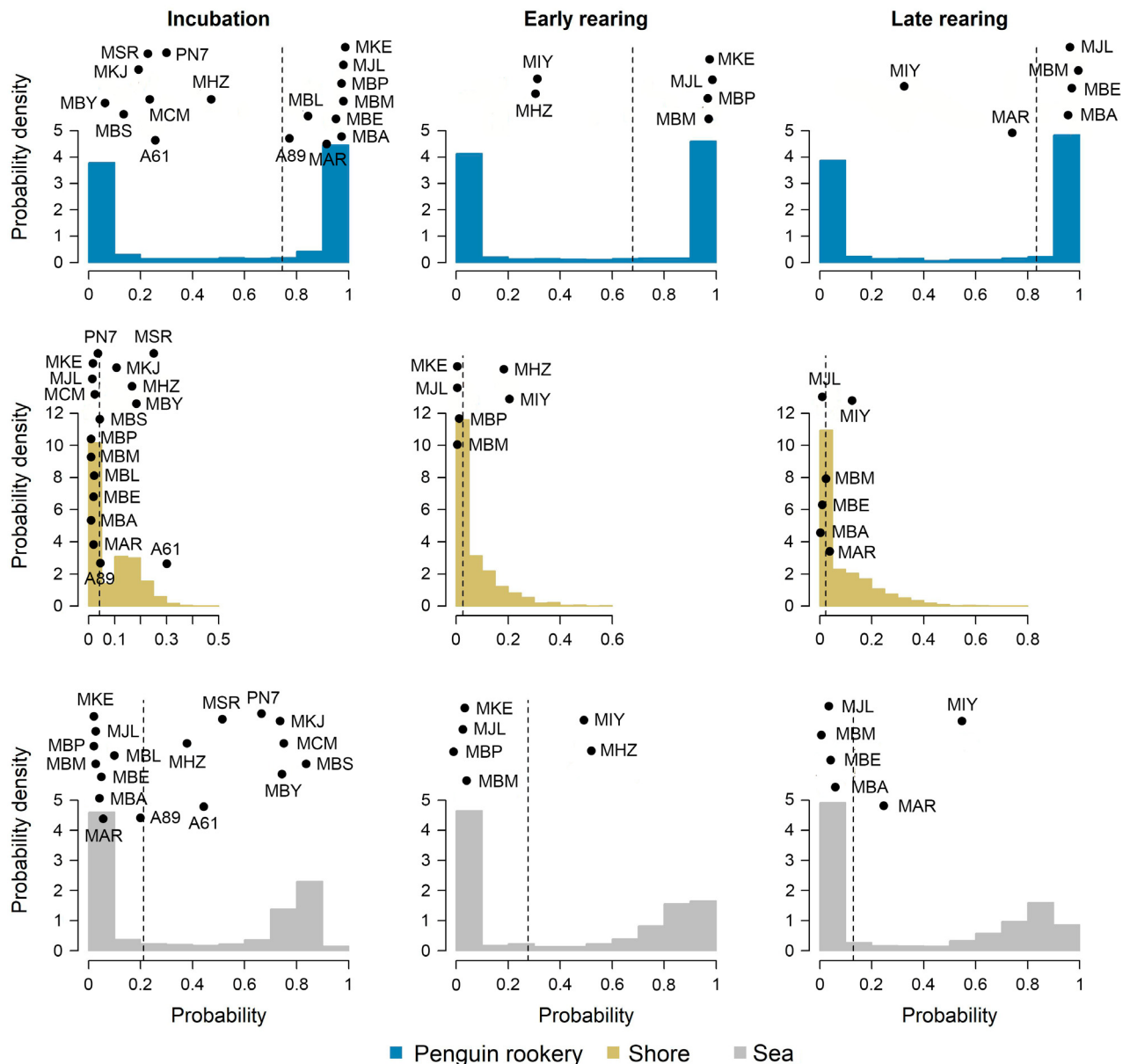The apparent contradiction in the results obtained through the 2 techniques could be partially ex-

Fig. 3. Probability of foraging in penguin rookeries, on shore, or at sea by breeding adult brown skuas *Stercorarius antarcticus* at the population level during the 3 stages of their breeding cycle. Dashed line: population median; black dots: median of the estimated probability distribution for each bird (see Table 1)

plained by the differential space use pattern among individuals, which means that some birds ingest mostly marine resources obtained directly from sea waters and shore, which are their main feeding grounds. Also, the birds feeding mostly on penguin rookeries may reduce their $\delta^{15}N$ values through the krill and fish they may feed on during their occasional foraging trips to the sea (see Figs. 1 & 2). Secondary ingestion of marine resources from the penguins' gut by birds that rely mostly on penguin rookeries can also contribute to the increase in the ingestion of marine resources indicated by stable isotopes. In the study area, the diet of gentoo and Adélie penguins is dominated by krill (Juáres et al. 2016). Brown skuas often kill penguin chicks, open their bellies and eat only their viscera, leaving the rest of the body (Hahn et al. 2005). Secondary ingestion would also explain the lack of correlation between the proportional use of penguin rookeries and blood $\delta^{15}N$ values (Fig. 5), as well as the time course decrease in $\delta^{15}N$ values of birds that visit very few locations at sea (Table 2).

Table 3. Isotopic values of red blood cells (RBCs) and plasma over 3 stages of the breeding cycle of brown skuas *Stercorarius antarcticus* from Potter Peninsula, King George Island, feeding mainly in penguin rookeries or at sea and on shore. C:N mass ratio is also shown as an indicator of lipid content. The *t*- and p-values show the comparison between consecutive breeding stages and the effect of sex, the fixed factors of the linear mixed-effects model. Values are means ± SD

|	n	C:N mass ratio	δ^{13}C	Estimate	*t*	p	δ^{15}N	Estimate	*t*	p
Penguin feeding										
RBC										
Incubation	9	3.24 ± 0.04	−23.0 ± 0.7	−1.4	−3.7	0.01	11.9 ± 0.8	−0.6	−2.7	0.4
Early rearing	4	3.25 ± 0.04	−24.8 ± 0.4	−2.1	−6.3	<0.01	10.8 ± 0.4	−1.7	−8.4	<0.01
Late rearing	5	3.22 ± 0.01	−25.2 ± 0.3				9.9 ± 0.4			
Male				0.5	1.19	0.27		0.9	2.2	0.06
Plasma										
Incubation	6	3.53 ± 0.07	−24.4 ± 0.6	−1.5	−9.4	0.06	11.5 ± 0.3	−0.4	−1.8	0.32
Early rearing	4	3.52 ± 0.07	−25.5 ± 0.3	−0.2	−0.7	0.59	11.1 ± 0.4	−1.6	−5.3	0.12
Late rearing	2	3.56 ± 0.01	−24.6 ± 0.7				9.8 ± 0.3			
Male				−0.4	−0.9	0.43		0.2	0.8	0.47
Sea/shore feeding										
RBC										
Incubation	8	3.23 ± 0.02	−23.4 ± 0.6	−1.6	−2.4	0.05	11.6 ± 0.7	−0.6	−0.9	0.38
Early rearing	2	3.21 ± 0.04	−24.7 ± 0.3				11.0 ± 0.4			
Late rearing	−									
Male				−0.1	−0.3	0.77		0.8	2.1	0.08
Plasma										
Incubation	6	3.49 ± 0.11	−24.2 ± 0.4	−1.1	−2.4	0.07	11.4 ± 0.4	−0.4	−0.7	0.51
Early rearing	2	3.56 ± 0.11	−25.6 ± 0.3				11.2 ± 0.1			
Late rearing	−									
Male				0.2	0.4	0.71		−0.2	0.4	0.68
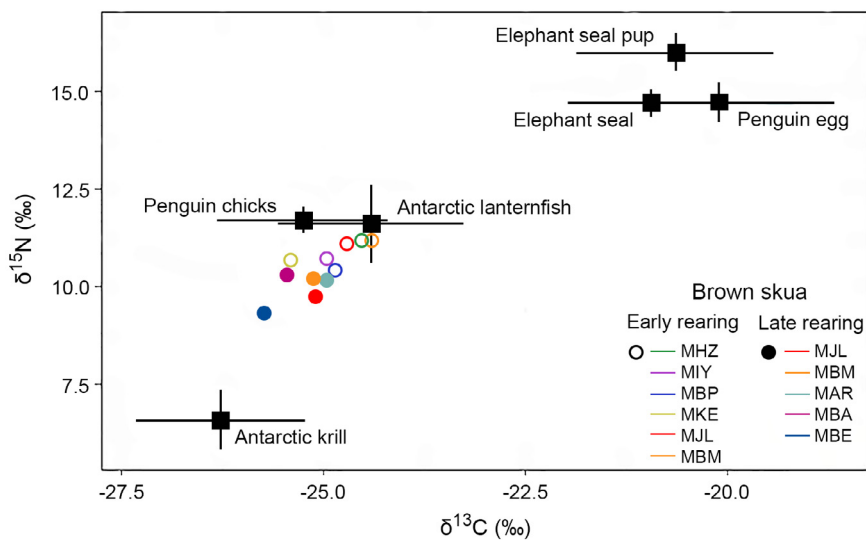
Fig. 4. Isotopic values (δ^{13}C and δ^{15}N) of red blood cells of brown skuas *Stercorarius antarcticus* (see Table 1 for details) during the early and late chick-rearing stages and of 5 food resources: Adélie penguin chicks *Pygoscelis adeliae*, gentoo penguin chicks *P. papua*, gentoo penguin eggshell membrane (Polito et al. 2009), elephant seal *Mirounga leonina* adults and pups (Ducatez et al. 2008, Hückstädt et al. 2012), Antarctic krill *Euphausia superba* (Kokubun et al. 2015), and fish *Electrona antarctica* (Polito et al. 2011). Isotopic values of food resources are represented as means ± SD corrected by their isotopic enrichment factors (Bearhop et al. 2002)

In light of the extremely low breeding success of the studied skua population (Graña Grilli 2014), one hypothesis is that the availability of food at the penguin colony is not enough, and some birds are forced to feed at sea as a result of territorial behaviour, thus reducing competition for the penguin resource. This hypothesis opens the question of why the birds feeding on penguin rookeries also show a high ingestion of marine resources. Poor body condition in brown skuas could induce the strategy of selecting krill among the available resources in the penguin colony, similar to the described selection of seal blubber by polar bears (Stirling & McEwan 1975). By behaving in this way, skuas may obtain the needed nutrients with a lower foraging energy cost than would occur if obtaining krill at sea. The ingestion of the penguin gut and its contents may also be a strategy of resource selection for nutritional purposes. Despite

Table 4. Bayesian stable isotope mixing model of the composition of the diet of brown skuas *Stercorarius antarcticus* during the early and late chick-rearing stages at Potter Peninsula, King George Island. Values are means ± SD (95 % credible intervals)

	Brown skua diet (%)	
	Early rearing	Late rearing
Penguin chick (*Pygoscelis adeliae* and *P. papua*)	33.7 ± 14.6 (5.5; 60.7)	23.0 ± 12.1 (2.9; 46.6)
Gentoo penguin eggshell membrane	6.2 ± 4.1 (1.0; 16.4)	5.2 ± 3.5 (0.8; 14.1)
Krill *Euphausia superba*	29.7 ± 6.5 (17.9; 43.2)	46.5 ± 6.2 (34.9; 59.3)
Antarctic lanternfish *Electrona antarctica*	16.7 ± 12.5 (1.7; 48.3)	13.6 ± 10.1 (1.5; 38.8)
Elephant seal *Mirounga leonina* pup	6.9 ± 4.7 (1.1; 19.0)	5.8 ± 3.8 (0.9; 15.7)
Elephant seal *M. leonina* adult	7.0 ± 4.9 (1.1; 19.5)	5.9 ± 4.2 (0.9; 16.5)

the energy content of krill and penguins being similar (~23.5 and 21.3 kJ g^{-1} dry mass, respectively; Janes 1997, Wang & Jeffs 2014, Schaafsma et al. 2018), their relative nutritional composition differs. The protein content is higher and lipid content is lower in krill (62 and 13 % of dry mass, respectively) (Wang & Jeffs 2014) than in penguins (45 and 38 % of dry mass, respectively) (calculated from Cherel et al. 1994). Keeping in mind that partially digested items may have lost part of their nutrients, the composition difference between the different resources — added to the cost of obtaining them — should be considered as a possible explanation for their selection.

Among the available food resources, krill could be selected by predators to compensate for a loss of the protein reserves needed to achieve optimum muscular mass before departing from the breeding site

(Graña Grilli et al. 2018). In contrast, lipid reserves may not be needed as a source of energy during migration, as brown skuas migrate over the sea where they can rest and feed regularly (Carneiro et al. 2016, Krietsch et al. 2017, Delord et al. 2018). In addition, krill has a high carotenoid content in different forms of astaxanthin (Yamaguchi et al. 1983), which is taken from the diet instead of from body reserves (Barbosa et al. 2013) and has an antioxidative and immune function (Miki 1991, Waldenstedt et al. 2003, Park et al. 2011). Therefore, krill could also be selected by skuas to compensate for a poor immunological condition, as indicated by the drop in the level of γ-globulins and IgY at the end of the breeding season (Ibañez et al. 2018).

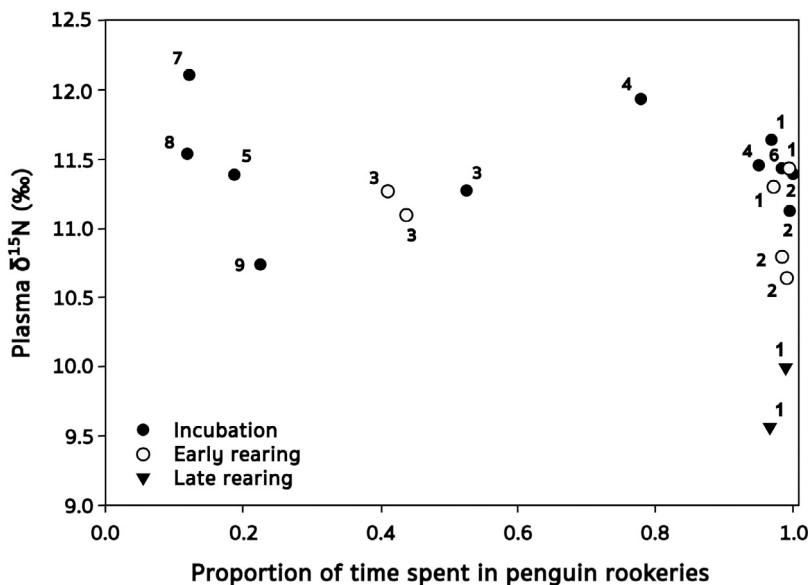The possible selection of krill as a food resource in a penguin rookery can only be inferred by the simultaneous use of 2 techniques. Movement analysis alone would lead us to the conclusion that the main food item for a portion of the skua's population is penguins, while stable isotope analysis would lead us to believe that marine resources are the predominant dietary item for the same population. Simultaneously sampling both kinds of data from the same birds suggests that krill is the dominant source of nutrients for self-feeding brown skuas, but that it is obtained through secondary ingestion from targeting penguin viscera, as low δ15N values are also found in birds specialising on foraging on penguin colonies. Similar to a previous study of skuas in a nearby colony (Carneiro et al. 2015), we also observed some longer trips to the sea during the late rearing stage; however, overall, we did not find a change in foraging areas through the breeding period.

Fig. 5. Relationship between proportion of time spent foraging at penguin rookeries and the plasma δ15N value of individual breeding brown skuas *Stercorarius antarcticus*. Numbers indicate belonging to the same pair (see Table 1 for details)

By contrast, we did find a partition of resources, with some birds feeding mostly at sea and others relying mostly on the penguin rookeries, from which the secondary ingestion of krill may constitute their main nutritional source. If the same birds eventually consumed the remainder of the penguin carcass, the $\delta^{15}N$ isotopic value of penguins should be higher. Why skuas would not use the whole carcass as a food resource is unknown but may be explained by theft of the remains by non-breeders or failed breeders, which was not considered in this work. Partitioning of foraging resources can be the result of the territory ownership of portions of the penguin rookeries by some brown skuas pairs (Hahn & Peter 2003, Hahn & Bauer 2008), which has also been seen as a cause of the exclusion of south polar skuas from terrestrial resources that may force them to forage at sea (Pietz 1987).

Since movement analysis through the proportion of locations on penguin rookeries vs. at sea and on shore does not suggest that the low availability of penguin chicks towards the end of the breeding period of brown skuas forces them to increase their foraging at sea, 3 feeding possibilities arise. Firstly, brown skuas may rely mostly on penguin carcasses as a food resource, in agreement with previous observations (Müller-Schwarze & Müller-Schwarze 1973, Carneiro et al. 2015). However, if that were the situation, we would expect it to be reflected in a change in the $\delta^{15}N$ of plasma (the tissue with the shortest turnover rate) indicating the use of higher trophic level prey, which is not what our results showed. Secondly, brown skuas may prey on even older penguin chicks and eat the prey contained in their stomachs, and the gut of a larger chick may contain more krill. The third possible explanation is that over time, skuas may increase their efficiency of foraging at sea, or that the decrease in $\delta^{15}N$ values relates to an increase in the body size of krill as summer progresses (Hewitt et al. 2004). Both effects could explain $\delta^{15}N$ values indicating more feeding at lower trophic levels without the corresponding increase in time spent at sea.

Our results highlight the importance of combining methods when studying diet to obtain a broader and more accurate view of the trophic ecology and feeding behaviour of seabirds. In our study, the use of only one method would have led to misleading conclusions about diet or feeding behaviour. Coherent results between the methods would have reinforced the evidence of the feeding strategy (Schultz et al. 2021); however, in our study, this combination of methodologies allowed us to hypothesize an interesting predator behaviour in brown skuas, consisting of eating a selection of specific parts of prey items to ab-

sorb the nutrients that some tissues provide instead of eating the whole prey. This trait deserves to be better studied, as it could shed light on how animals cope with their nutrient needs and deficiencies over the different stages of the annual cycle.

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