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ORIGINAL PAPER

Diet of the Brown Skua (*Stercorarius antarcticus lonnbergi*) at Hope Bay, Antarctic Peninsula: differences between breeders and non-breeders

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Abstract

Top predators exhibit a critical role in ecosystem functioning and in the stability of the food web, so research on diet is relevant to understand their foraging behavior. Seasonal variation in diet and prey selection may be the result of fluctuations in the physiological demands during the different annual life cycles, and ecological factors such as resource availability, which may influence the foraging behavior. Moreover, the competition for the feeding territories between conspecifics in a population or with other predators may also lead to diversification of the diet. In this work, we determined the diet of breeding and non-breeding Brown Skuas (*Stercorarius antarcticus lonnbergi*) at Hope Bay, Antarctic Peninsula, to understand prey selection and the feeding habits of groups with different physiological and energy demands. To assess the breeders' diet, 204 pellets were collected near the nests, while for non-breeders, 330 pellets were obtained from different areas where they usually group, and prey items were determined. Pellet dimensions were larger in non-breeding skuas. Breeding skuas' pellets showed a higher content of energy-rich items such as penguin eggs, fishes and molluscs, while in non-breeding skuas, pellets consisted mainly of penguin feathers and bones. The differences in diet between the groups may be a consequence of the supplementation of the food obtained on land by traveling to the ocean by breeding skuas, in order to compensate the energetic demands during reproduction. Our results highlight differences in the feeding habits and prey selection, as well as a variation in the flexibility of the foraging strategy of both groups.

Keywords Brown Skua (*Stercorarius antarcticus lonnbergi*) · Breeding · Non-breeding · Diet · Pellets · Antarctica

Introduction

Seabirds are integral components of marine ecosystems and are indicators of changes in the marine environment (Barret et al. 2007). Studies of the diet and foraging ecology of top predators are important to provide useful insights into changes in food resources in the wider environment (Furness and Camphuysen 1997). Moreover, diet studies provide information about the foraging behavior of the top predators and their preference for different preys. Depending on the tissue analyzed and the methods employed, diet studies may also provide retrospective diet insights (Barret et al. 2007).

Reproduction imposes very different demands in terms of energy and nutrient balance compared with the non-breeding period (Williams 2018). As central-place foragers during the breeding season, seabirds have to adjust their feeding behavior to satisfy both their energetic requirements and those of their offspring (Weimerskirch et al. 2000; Phillips et al. 2004b; Hahn et al. 2007; Navarro et al. 2009; McLeay et al. 2010). As a result, within a single breeding season, foraging strategies may also vary in response to fluctuations in prey availability, a switch from incubation to chick rearing and changes in the nutritional demands of growing chicks (Shaffer et al. 2003; Hipfner et al. 2013). Moreover, the diet and feeding habits of birds may change depending on the breeding status, or because of other intrinsic factors such as age, experience and sex (Williams 2018).

Paloma Borghello and DiegoSebastián Torres have substantially contributed equally in the fieldwork and data analysis

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Brown Skuas (*Stercorarius antarcticus lonnbergi*) are top predator seabirds that breed in subantarctic islands and in Antarctica (Ritz et al. 2008; Graña Grilli 2015; Graña Grilli and Montalti 2015). Before the Antarctic summer begins, Brown Skuas migrate from winter locations to breeding localities in Antarctica (Phillips et al. 2007; Krietsch et al. 2017). Before the eggs are laid, during incubation and in the brooding stage, males undertake a greater share of foraging to feed the females and chicks (Burton 1968; Devillers 1978). In breeding localities, Brown Skuas have remarkably diversified diets (Reinhardt et al. 2000; Montalti 2005). They are regarded as opportunistic predators, scavengers and kleptoparasites which enable them to exploit a wide range of food resources according to their temporal and spatial availability (Furness 1987; Moncorps et al. 1998; Mougeot et al. 1998; Reinhardt et al. 2000; Graña Grilli and Montalti 2012, 2015; Graña Grilli et al. 2014; Graña Grilli 2015). These birds may also scavenge at refuse tips from the improper waste management on the bases or refuges (Reinhardt et al. 2000). Although opportunistic feeding behavior has been described in this species, they can often depend on fewer types of prey; primarily seal carcasses and placentae, or eggs, chicks or adults of seabirds nesting in nearby colonies (Pietz 1987; Reinhardt et al. 2000); also, there are individuals that specialize on catching small petrels at night (Young et al. 1988; Ryan and Moloney 1991; Moncorps et al. 1998; Mougeot et al. 1998; Ryan et al. 2009). In several Brown Skua populations, some birds establish feeding territories in adjacent areas to penguin or petrel colonies, whereas others forage over a wide area whivh they do not defend from other conspecifics or where no competition with other predators exists (Trivelpiece et al. 1980; Pietz 1987; Hahn and Peter 2003). During the reproductive season, breeding individuals exhibit flexible foraging strategies (Carneiro et al. 2014). At the beginning of the season, during incubation and the early rearing of chicks, most parents forage on prey captured ashore versus at sea (Trivelpiece et al. 1980; Trivelpiece and Volkman 1982; Graña Grilli and Montalti 2012; Graña Grilli et al. 2014). Moreover, it has been reported that, by the late rearing period, when the availability of penguins had diminished, Brown Skuas were able to supplement the food obtained on land by traveling to the ocean (Carneiro et al. 2014, 2015), and marine resources become more abundant in the diet, including krill (*Euphausia superba*), fish and molluscs (Graña Grilli et al. 2014).

At Bahía Esperanza/Hope Bay, Antarctic Peninsula, there exists one of the larger Adélie Penguin (*Pygoscelis adeliae*) breeding colonies (about 104,139 breeding pairs) and two small breeding colonies of Gentoo Penguin (*Pygoscelis papua*) during the months of November to February (Santos et al. 2018). Brown Skuas breed near these colonies and their breeding cycle chronology (incubation, hatching and rearing) is in synchrony with the Adélie's and Gentoo's. Thus, in these areas where penguins are breeding, skuas can successfully exploit (with respect to amount and accessibility) this food source (Trivelpiece et al. 1980; Young 1994).

Regarding to foraging and prey selection, it is also recognized that individuals within the same species can often have different dietary niche preferences even in the same environment, i.e., they can show individual diet specialization due either to genetic differences (e.g., sexually dimorphic morphological feeding adaptations) or because of variation in learned behaviors (Bolnick et al 2003; Mackley et al. 2011). One of the less studied factors affecting foraging strategy is reproductive status. Failed breeders often continue to associate with the colony, operating as central-place foragers but expand their foraging areas (González-Solís et al. 2007). They may be partially or completely segregated from breeders, probably to avoid competition (Phillips et al. 2017). Although a generalist diet and flexible foraging strategies have been well reported for this species at different colonies (Mougeot et al. 1998; Reinhardt et al. 2000; Phillips et al. 2004a; Ryan et al. 2009; Graña Grilli and Montalti 2012), little is known about the feeding habits of individuals exposed to different energy demands when sharing the same feeding territory. Considering this, the aim of this study was to assess the diet groups of Brown Skuas with different reproductive status (breeders and non-breeders) in order to elucidate differences in the feeding habits and prey selection (in terms of diversity) to supply the nutritional requirements under different physiological demands.

Materials and methods

The study was conducted during a single breeding season (from November 2015 to February 2016) at Bahía Esperanza/Hope Bay (63°24′S, 57°01′W; from SCAR-MarBIN Portal at https://www.scarmarbin.be/SearchGazetteer.php, accessed 12 February 2018), Antarctic Peninsula (Fig. 1). Brown Skuas breed in this region (from November to February) with a high avian diversity (Coria and Montalti 1993). During this season, the total number of Brown Skua breeding pairs ($n = 23$) was determined by counting the active nests. On the other hand, non-breeding skuas ($n = 83$) were counted in the resting areas near the sea and ponds, where they are usually grouped in clubs by the middle of the breeding season. By this period of the season, the population of non-breeding skuas reaches its maximum number of individuals since it is composed of juvenile non-breeders and failed breeders in addition to sabbatical or senescent individuals.

Upon arrival at the study site (late November), the area surrounding the skuas' nests was cleaned of pellets in order to avoid the collection of pellets belonging to previous seasons. All those pellets were discarded and the fresh pellets for analysis were then collected near active nests. As some

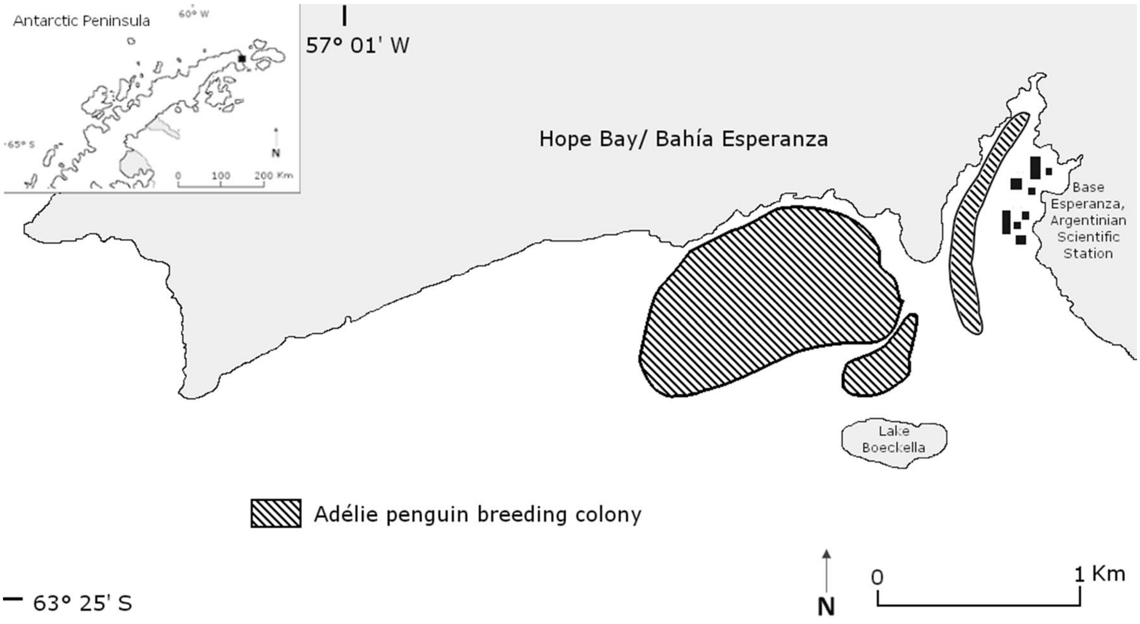

Figure 1 Study site located at Bahía Esperanza/Hope Bay, Antarctic Peninsula (63°24′S, 57°01′W)

of the nests studied failed during incubation or during the early rearing of the chicks, it was not possible to collect pellets from all the nests of the colony during the entire breeding season. A total of 204 fresh regurgitated pellets were collected from the proximity of the nests every 5 days during the incubation, early and late rearing stages, and 330 from the resting areas where the clubs were grouped. As breeders often visit non-breeders´ clubs, it is not possible to ensure that all the pellets collected for this group belonged to non-breeders. Once in the laboratory, the pellets were dried at room temperature, placed in nylon stockings and stored in cardboard boxes until their analysis. Pellet dimensions (length, width and height) were determined using digital calipers and the volume of regurgitated pellets was calculated by using the equation $V = ¾\pi \times (a \times b \times c)$, where a, b and c are the ratios of axes x (length), y (height) and z (width) (see Fig. 2b). Then, each pellet was placed into a Petri dish and disaggregated to separate contents. The material was sorted into prey items under a binocular microscope (×4). Contents were assigned to the following general prey

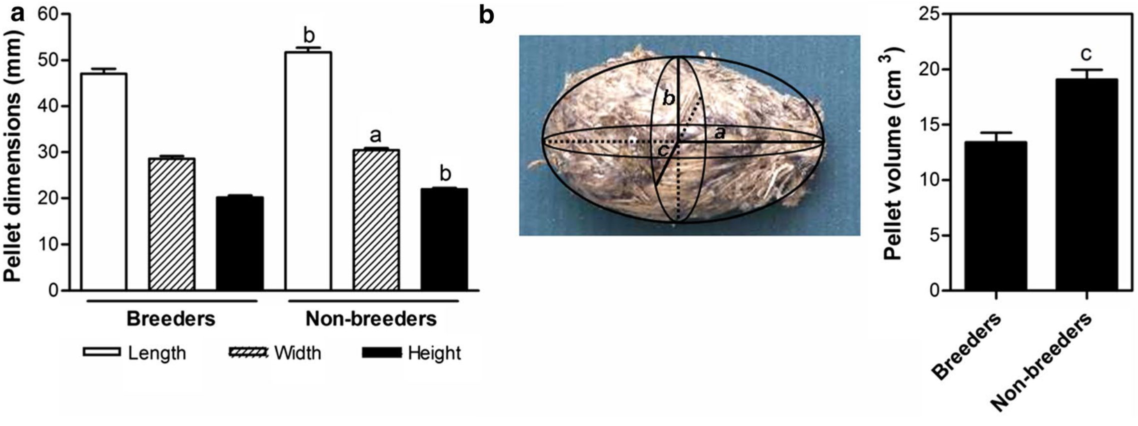

Figure 2 Dimensions of regurgitated pellets of breeding and non-breeding Brown Skuas (*Stercorarius antarcticus lonnbergi*) at Bahía Esperanza/ Hope Bay, Antarctic Peninsula, during the breeding season (2015–2016). **a** Length (mm), width (mm) and height (mm) for each group. **b** Volume of regurgitated pellets of both groups was calculated by using the equation $V = ¾\ \pi \times (a \times b \times c)$, where a, b and c are the ratios of axes x, y and z, respectively. Data are represented as mean ± SE for the volume (cm^3) of both groups. Statistical results correspond to p values calculated by the Mann–Whitney test ($a = p < 0.05$, $b = p < 0.01$ and $c = p < 0.001$) for both groups

categories: penguin, flying birds (FBs), fish, mollusc and mammal. Particular dietary items were identified and classified into subcategories: penguins [feathers (PF), bone (PB) and egg-shell fragments (PES)], FBs [feathers (FBF), bone (FBB) and egg-shell fragments (FBES)], fish [otoliths, scales, crystallines and fish vertebrae (FV)], mammal (in particular, fur seals), and, regarding molluscs, gastropods were identified by the presence of shell remains from limpets, and cephalopods through the presence of beaks.

Most of the fish otoliths were identified to species level by using specialized literature (Hetch 1987; Reid 1996). Otolith's longitudinal (OW) and vertical (OL) axes were measured using a binocular microscope with scale (× 416) and total length (TL) of fishes was estimated by using the appropriate formula for each species (Hetch 1987). The total length of *Pleuragramma antarcticum* was estimated as $\mathrm{TL} = 99.6 \times \mathrm{OL}^{1.05}$ (Hetch 1987).

Bone remains of flying birds (most of them tarsi) found in pellets were used to determine the species consumed by the skuas. The tarsi and other bone remains were compared against the tarsus and complete skeletons, respectively, of all the antarctic flying birds preserved in the Osteological Collection of the La Plata Museum, Natural Science Faculty and Museum, La Plata National University, Argentina. In addition, egg remains found in the Brown Skua diet were characterized by their comparison with eggs preserved in the Ornitological Collection of the La Plata Museum. Brown Skuas and Kelp Gull (*Larus dominicanus*) eggs are very similar in their tone and coloration, which makes their identification from small fragments very difficult. Brown Skua eggs are stone-brown and heavily marked, while Kelp Gull eggs are large and gray-green with dark brown spots and blotches. On the other hand, the eggs of the Snowy Sheathbill (*Chionis alba*) are pyriform, or pear-shaped, with a creamy white base color speckled with gray or brown. Based on the comparison of these patterns, the eggshell remains found could be assigned to each of these species. Feathers of penguins and FBs were differentiated by the morphology of the rachis and the length of the barbs.

Results of the general prey categories and particular dietary items of breeding and non-breeding Brown skuas were expressed as frequency of occurrence (FO), which was calculated by the formula $\mathrm{FO} = (f_i/\mathrm{N})$, where f_i is the number of pellets with item *i* and N is the total number of pellets. Also, the relative frequency of food items $\mathrm{RF} = (fi/\Sigma fi)$ was estimated as the number of times food item *i* was found among pellets as a ratio of all food items found. Although FO indicates how common an item in the pellet is, RF provides a better indication as to how often an item is consumed because it accounts for multiple items being found in a pellet (De Villa Meza et al. 2002; Malzof and Quintana 2008). Pebbles were not taken into account for the FO or RF analysis, as they are not considered a dietary item.

To assess statistical differences in the dimensions of pellets, a Mann–Whitney *t* test for the parameters measured (length, width and height) and volume was conducted. A $p < 0.05$ was considered a significant difference. To test for differences in the consumption of the food items between breeders and non-breeders, the Chi-square (χ^2) test was performed. These results have been presented in the text as: Chi-square test (χ_{df}), *p* value, where *df* = degrees of freedom. Moreover, to examine diet according to breeding status, a canonical correspondence analysis (CCA) was used. This is an ordination method which combines the algorithm of correspondence analysis and a multiple regression analysis on explanatory variables (ter Braak 1986). To perform the CCA, we considered the volume of each pellet and the status of the birds (factor with two levels: breeder and non-breeder) as predictors. The significance of the explanatory variables used was assessed using ANOVA-like permutation tests (999 permutations). Analyses were conducted with the *vegan* package (Oksanen et al. 2015) in R 3.2.2 software (R Core Team 2015). Based on the pellets collected, the trophic niche breadth was calculated for breeding and non-breeding Brown Skuas. For this, we used Levin's index (Colwell and Futuyma 1971), which measures how uniformly resources are being utilized by each studied group. First, Levin's index of niche breadth was calculated as $\mathrm{B} = 1/\Sigma \rho i^2$, where *pi* is the proportion of individuals found using resource *i*. Then, standarized Levin's index (*BA*) was calculated as $BA = (\mathrm{B}-1)/(n-1)$, where *n* is the total number of food items for the species of interest. Also, the overlap of the trophic niche was estimated using the overlap percentage (Krebs 1989).

Results

Significant differences were observed in pellet size between groups. Non-breeders' pellets had larger dimensions than those from breeders (mean ± SE; breeders' length: 47.08 ± 1.075 mm, width: 28.60 ± 0.555 mm and height: 20.16 ± 0.451 mm, $n = 204$; non-breeders length: 51.69 ± 0.981 mm, width: 30.45 ± 0.468 mm and height: 21.92 ± 0.377 mm, $n = 330$ (Mann–Whitney *t* test length $p = 0.0049$, width $p = 0.0249$ and height $p = 0.0038$) (Fig. 2a). Accordingly, the volume of each pellet was significantly higher in non-breeders (mean ± SE; breeders: 13.41 ± 0.8472 cm^3, $n = 204$ and non-breeders 19.05 ± 0.8934 cm^3, $n = 330$, Mann–Whitney *t* test $p < 0.0001$) (Fig. 2b).

The total number of dietary items found was 421 for breeders and 596 for non-breeders skuas (Table 1). In some cases, pellets contained more than one particular item from each category, such as otoliths and fish vertebrae for fishes, for example. In both groups, pellets contained penguin,

Table 1 Food item categories and particular dietary items recorded in the regurgitated pellets of breeding and non-breeding Brown Skuas at Bahía Esperanza/ Hope Bay, Antarctic Peninsula, during the breeding season 2015–2016

Diet categories/ Dietary items	Breeding ($n=204$)			Non-breeding ($n=330$)			Between breeding and non-breeding Brown skuas (considering all analyzed pellets)	
	NO	FO	RF	NO	FO	RF	*X*	*p*
Penguin	199	0.98	0.84	323	0.98	0.87	0.0624	0.8027
Feathers	133	0.65	0.32	301	0.91	0.50	547.301	< 0.0001[c]
Bones	117	0.57	0.28	159	0.48	0.26	53.602	0.0206[a]
Eggshell	102	0.50	0.24	62	0.19	0.10	629.042	< 0.0001[c]
FB	15	0.07	0.04	22	0.07	0.04	0.0924	0.7616
Feathers	0	0.00	0.00	1	0.003	0.002		
Bones	8	0.04	0.02	9	0.02	0.01	0.7648	0.3818
Eggshell	10	0.05	0.02	19	0.05	0.03	0.2351	0.6278
Fish	31	0.15	0.09	28	0.08	0.07	57.785	0.0162[a]
Otoliths	11	0.05	0.03	15	0.05	0.02	0.1683	0.6816
Vertebrae	21	0.10	0.05	16	0.05	0.03	62.117	0.0127[a]
Crystallines	1	0.004	0.002	6	0.02	0.01	0.0145	0.9041
Scales	4	0.02	0.010	4	0.01	0.01		
Mammal	0	0.00	0.00	7	0.02	0.01		
Fur seals	0	0.00	0.00	7	0.02	0.01		
Mollusc	13	0.06	0.03	6	0.02	0.01	91.328	0.0025[b]
Gastropods	13	0.06	0.03	4	0.01	0.01	102.615	0.0014[b]
Cephalopods	0	0.00	0.00	2	0.01	0.003	0.0302	0.8618
Total items	421			596				

Statistical results were analyzed for both groups using Chi-square test (χ^2) (a = $p<0.05$, b = $p<0.01$ and c = $p<0.001$)

Data are summarized as *n* number of analyzed pellets, *NO* number of occurrences, *FO* frequency of occurrence, *RF* relative frequency.

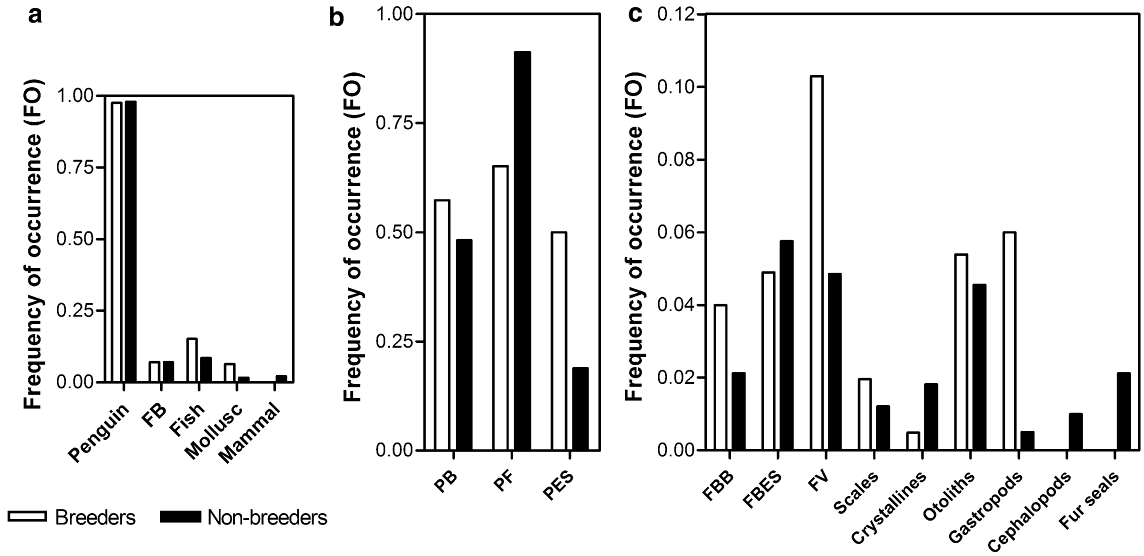

Figure 3 Frequency of occurrence (FO) of **a** dietary categories **b** particular dietary items and **c** minor dietary items found in regurgitated pellets of breeding ($n=204$) and non-breeding ($n=330$) Brown Skuas. *PB* penguin bones, *PF* penguin feathers, *PES* penguin eggshell, *FBB* flying birds bones, *FBES* flying birds eggshell, *FV* fish vertebrae

FB, fish and mollusc remains, while in the non-breeding group only mammal items were found (Fig. 3a; Table 1). Despite both groups demonstrating a large consumption of penguins, differences in the minor items such as fish, mollusc and mammal categories were observed. Breeding Brown Skuas showed a significantly higher FO in fish (Chi-square test $\chi_1 = 5.778$, $p = 0.0162$) and Mollusc (Chi-square test $\chi_1 = 9.132$, $p = 0.0025$) categories, while only in non-breeding skuas were mammal remains, mainly fur seals, found (Table 1). Analysis of the particular dietary items of each prey category showed differences between the groups (Fig. 3b, c). The frequency of occurrence of PB and PES was higher in breeding Brown Skuas (PB: Chi-square test $\chi_1 = 5.360$, $p = 0.0206$ and PES: Chi-square test $\chi_1 = 62.90$, $p < 0.0001$) (Fig. 3b, c; Table 1). Also, a significantly higher FO of FV was determined in the breeding group (Chi-square test $\chi_1 = 6.211$, $p = 0.0127$ vs. non-breeders), although no differences were observed in other particular items of this category (otoliths, crystallines and scales) (Fig. 3c).

A total of 26 fish otoliths were recovered (11 from breeding skuas and 15 from non-breeding). Three fish species were identified, *Pleuragramma antarcticum*, *Electrona antarctica* and *Lepidonotothen nudifrons*. The most frequent was *P. antarcticum* which appeared in 23 pellets (10 in breeders and 13 in non-breeders). The length (mean ± SE) for fish ingested by breeding birds was 190.8 ± 23.74 mm and 212.15 ± 8.01 mm for non-breeders, and no differences were observed in the dimensions of fishes consumed between groups. Among the mollusc category, gastropods were predominant in the breeding Brown Skua diet compared with the non-breeding skuas (Chi-square test $\chi_1 = 10.26$, $p = 0.0014$) and cephalopods were only found in the non-breeding group (Fig. 3c; Table 1).

Flying bird remains were found in pellets of both groups. No differences were observed in this category (Chi-square test $\chi_1 = 0.092$, $p = 0.7616$) (Fig. 3c; Table 1). Different species could be determined by comparison of the bone remains found with those preserved in our collection, such as Wilson's Storm Petrel (*Oceanites oceanicus*), Snowy Sheathbill, Kelp Gull, Black-bellied Storm Petrel (*Fregetta tropica*) and Brown Skua (remains from chicks), while six bone samples could not be identified (Table 2). Among them, Wilson's Storm Petrel was predominant in pellets. When determining the eggshells fragments from FBs category, we observed the remains of Snowy Sheathbill eggs. However, in some cases, it was not possible to assess the species due to the small size of the eggshell remains and to the similarity in the color between Brown Skua and Kelp Gull eggs.

The niche breadth of breeding Brown Skuas ($B_A = 0.223$) was at least twice the value of that of non-breeding ($B_A = 0.110$) birds, with an overlap of 100%.

Table 2 Species, number and frequency of occurrence of flying birds consumed by Brown Skuas at Bahía Esperanza/ Hope Bay, Antarctic Peninsula

Flying bird species	Breeding ($n = 204$)		Non-breeding ($n = 330$)	
	NO	FO	NO	FO
Wilson's Storm Petrel (*Oceanites oceanicus*)	2	0.01	3	0.01
Kelp Gull (*Larusdominicanus*)	0	0.00	2	0.01
Snowy Sheathbill (*Chionis alba*)	2	0.01	0	0.0
Black-bellied Storm Petrel (*Fregetta tropica*)	2	0.01	0	0.0
Unidentified	2	0.01	4	0.01

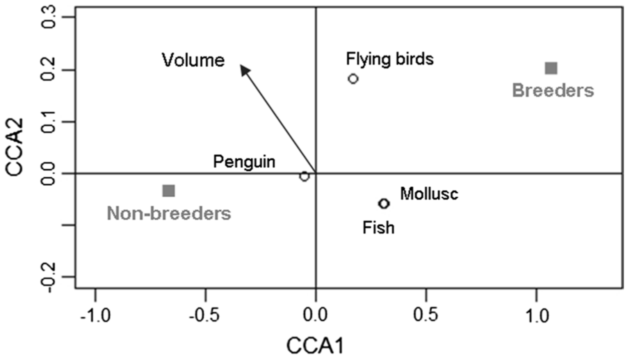

Figure 4 Ordination diagram generated by the Canonical Correspondence Analysis (CCA) of Brown Skua status in relation to dietary categories. *Circles* represent each dietary category (Penguin, Flying birds, Fish and Mollusc). The *crosses* represent the mean of each status "Breeder or Non-breeder" and its relation to the categories

The CCA showed an association between the status of the skuas and the predominance of prey (Fig. 4). Both breeding and non-breeding pellets were dominated by penguin remains; however, in breeding skuas, a higher abundance of fish and mollusc remains occurred. Axis I and II of the CCA explained 86.64% and 13.35% of the variance, respectively. This result was tested with an ANOVA, and significant differences were assessed between status (ANOVA: $F_{1,4} = 4.702$, $p = 0.027$). In addition, the volume of pellets as a continuous variable showed no effect on response variables suggesting that volume was independent of both variables.

Discussion

Foraging strategies of seabird species often vary considerably between and within individuals. This variability is influenced by a multitude of factors including age, sex, stage of annual life cycle, reproductive status, individual specialization and environmental conditions (Jakubas et al. 2018). Regarding diet selection, individuals within the same species can often have different dietary niche preferences even in the same environment (Williams 2018). In the present study, regurgitated pellets of two groups of Brown Skuas (breeders and non-breeders) were used to determine the diet and feeding habits of individuals exposed to different physiological and energy demands. This study revealed that, depending on the reproductive status, Brown Skuas are able to adapt their foraging behavior in order to supplement their diet throughout the reproductive season. Our observations agree with others previously reported, in which, during the reproductive season, breeding skuas supplement their diet with marine resources. Moreover, in this breeding location, there are no potential predators; nevertheless, breeding Brown Skuas share the feeding niche with a large number of non-breeding conspecifics. Notwithstanding, both groups exhibited different feeding strategies and prey selection.

Reproduction is a process characterized for its high physical effort and energy demand (Gustafsson et al. 1994; Hanssen et al. 2005). Within a single breeding season, adult seabirds may adopt temporally flexible foraging strategies to satisfy the different energy and time demands of incubation and chick rearing and of both their own energetic requirements and those of their offspring (Weimerskirch et al. 2000; Phillips et al. 2004b; Hahn et al. 2007; Navarro et al. 2009; McLeay et al. 2010). As a result, a shift in the foraging strategies occurs in response to fluctuations in prey availability, the switch from incubation to chick rearing and changes in the nutritional demands of growing chicks (Shaffer et al. 2003; Hipfner et al. 2013). Conversely, non-breeding individuals are not exposed to the pressure of feeding offspring, and thus to a lower energy demand. Overall, these may be the main reasons for expecting differences in the diet and feeding habits of these groups. We observed differences in the pellet dimensions (length, width and height) and volume, being larger in non-breeding skuas. This may be related to differences in the feeding behavior of these groups. Young (1994) previously reported a variation in the feeding attempt frequency between breeding and non-breeding Brown Skuas. First, because nests and young chicks need to be defended, or eggs incubated continuously, skuas only conduct short breaks away from the nest area. This constraint on foraging is important and may account for the preponderance of opportunistic feeding compared with the sustained feeding conducted by some non-breeding skuas which have more time available for feeding. Moreover, pellet size may be related not only to the feeding timing but also to the amount of non-digestible tissue taken in during feeding (Votier et al. 2002, 2003). Thus, the difference in pellet size could be a direct consequence of the availability of time for feeding as well as to an increased scavenging activity in non-breeding skuas.

In Antarctic breeding localities, Brown Skuas have a generalist diet (Furness 1987; Reinhardt et al. 2000; Graña Grilli and Montalti 2012; Graña Grilli et al. 2014; Graña Grilli 2015; Graña Grilli and Montalti 2015). Here, diet based on regurgitated pellet analysis showed that both groups shared mostly a common diet, with similar proportions in the predominant items, while significant differences were observed for minor items. Penguins were the main prey consumed by both groups, followed by fishes, molluscs and FBs. Our results are similar to those found at Deception Island (Graña Grilli and Montalti 2012) and differ from those at Cierva Point, Antarctic Peninsula, where the most consumed prey were fishes (Malzof and Quintana 2008). Interestingly, differences in some particular items between groups were assessed, such as penguin eggshell, fish vertebrae and gastropods. The FO of these items was significantly higher in breeding skuas, indicating a shift in prey selection copmared with the non-breeding individuals. As has been previously reported at breeding localities, they usually depend on fewer prey types, primarily eggs and chicks or adults of seabirds nesting in nearby colonies (Pietz 1987; Reinhardt et al. 2000). At Hope Bay, there is one of the largest Adélie Penguin breeding colonies and also two small Gentoo Penguin breeding colonies, indicating the great availability of food resources for both groups. Our results suggest that breeding skuas, despite the high availability of penguins, select penguin eggs and different marine resources, such as fishes and molluscs. A possible explanation for this is that the breeders exhibit a higher flexibility in their foraging strategy that enable them to use different prey compared with the non-breeding skuas. To further support this idea, previous reports have indicated that breeding Brown Skuas spend more time foraging at sea than in the penguin colony (Carneiro et al. 2014), and also, in the course of the breeding cycle, fishes become relevant in their diet (Graña Grilli and Montalti 2014).

Foraging strategies may also vary as a response to prey availability which is driven by prey biology, environmental conditions and/or prey depletion near the colony due to intense foraging (“Storer–Ashmole’s halo”; Hipfner et al. 2013). The use of fish as prey at this location was lower than that observed at Cierva Point (Malzof and Quintana 2008), and higher than at Deception Island (Graña Grilli and Montalti 2012). The differences in the diet between locations may be due to a variation in the availability of penguins. At Cierva Point, there are two small breeding colonies of Chinstrap (*Pygoscelis antarctica*) and Gentoo Penguins (Quintana 2000). This fact may force skuas to feed more frequently at sea in this location, while at Hope Bay as at Deception Island, because the great availability of penguins as prey, skuas may be less pressured to do so (Young 1963; Trillmich 1978; Young and Millar 1999; Carneiro et al. 2014). Interestingly, in constrast to these reports, we observed that, despite the great availability of penguins, breeding skuas show a greater consumption of marine prey.

Predation on other seabirds, mainly eggs and chicks of small petrels, is a common foraging strategy of Brown Skuas (Furness 1987; Pietz 1987; Moncorps et al. 1998; Malzof and Quintana 2008). Concerning this category, we did not address differences between groups. The most abundant prey found was Wilson's Storm Petrel, suggesting that, among flying birds, this species contribute significantly to the diet of skuas. Also, in non-breeders' pellets, eggs of other bird species, such as Kelp Gulls and conspecifics, were observed.

The number of occurrences of Kelp Gulls in skua pellets from both groups (breeders and non-breeders) was lower in our study compared with studies at other locations (Malzof and Quintana 2008; Graña Grilli and Montalti 2012). Nevertheless, the frequent occurrence of remains (bones) of this species in the field suggests that their contribution to skua diet was underestimated in our results. The low occurrence of this species in pellets is not representative of their abundance at Hope Bay (Coria and Montalti 1993), on the basis that skuas feed preferentially on the most abundant and readily obtainable prey species (Norman and Ward 1990; Mougeot et al. 1998).

Brown Skuas establish feeding–breeding territories near breeding colonies of pygoscelid penguins which are exploited as a food resource by the territorial pairs. These delimited territories are defended against other predators (Kelp Gulls or South Polar Skuas *S. maccormicki*) and conspecifics (Trivelpiece et al. 1980). In Antarctic regions where Brown and South Polar skuas breed in sympatry, it has been reported that Brown Skuas exclude South Polar Skuas from feeding territories thus monopolizing land resources, while the South Polar feeds mainly on marine resources (Malzof and Quintana 2008; Graña Grilli and Montalti 2015). In addition, conspecifics frequently compete for the best feeding areas. Because of the great availability of food resources within the breeding skuas' feeding territories, non-breeders invade the territorial boundary to feed (Furness 1987). At Hope Bay, because of the great size of the penguin colony, breeding and non-breeding skuas are found surrounding this colony and share the feeding areas without any territorial delimitation (personal observations), so we expected to find a great overlap in the trophic niche breath between the groups. We observed that the trophic niche breadth between the groups is completely overlapped (100%); however, breeding skuas have a broader dietary niche than non-breeders. Although the differences found in the diets of the two groups and the overlap of the trophic niche, it may not be indicative of competition or exclusion between the groups because the food resource most used was that with greater availability (Colwell and Futuyma 1971). The CCA analysis evidenced a predominance of marine resources in breeding skua pellets, indicating that breeders may have preferred to feed on marine prey, broadening their trophic niche to supplement their nutritional requirements. Overall, these observations reflect the flexibility in the foraging strategy and the capacity of breeding Brown Skuas to take advantage of different resources in the breeding territory (Reinhardt et al. 2000; Malzof and Quintana 2008; Graña Grilli and Montalti 2015).

Despite the overlap in the feeding territory of both groups and the great availability of penguins as a resource at the study area, our results suggest that breeders consumed marine resources in greater quantity. Moreover, our study highlights the flexibility and variability in the foraging behavior and diet of breeding skuas. Contrasting with other studies that have shown that breeding skuas are able to exclude other species (Malzof and Quintana 2008; Graña Grilli and Montalti 2015) or conspecifics (Trivelpiece et al. 1980), in this location both groups are able to coexist. Although both groups are able to share the same resources, they use them differently, indicating that breeding skuas develop adaptive behavior and feeding strategies, optimizing the use of the marine resources to satisfy both their energetic requirements and those of their offspring, whereas in non-reproductive individuals this behavior is probably not so frequent.

We are aware of possible limitations of our study. We did not try to distinguish individuals belonging to each group, and also, as breeders often visit non-breeder clubs, it was therefore possible that not all pellets collected from clubs were necessarily from non-breeders. Thus, we cannot be sure of the amount of breeders' pellets that could be collected from the resting areas of the non-breeders, so these results must be considered with caution. Considering this, our observations could be improved by identifying individuals and monitoring these groups to compare feeding strategies throughout the reproductive season. Future studies on the foraging specialization of Brown Skuas, supported by other methodologies (e.g., GPS tracking and stable isotope ratio analysis) could be useful for investigating the foraging strategies of these two groups.

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Compliance with ethical standards

Conflicts of interest No conflict of interests exists between the authors of this work.

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