



# Pellet analysis evidences flexibility in the diet of Brown Skua (*Stercorarius antarcticus*) during breeding at Esperanza/Hope Bay (Antarctic Peninsula)

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## Abstract

At Esperanza/Hope Bay, Antarctic Peninsula, breeding Brown Skuas (*Stercorarius antarcticus*) coexist with a breeding colony of Adélie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguins. Previously, we reported that the principal prey consumed by Brown Skuas was penguin, however, the contribution of marine resources to their diet was high. Besides, the number of conspecifics that compete for this resource gradually increases across the season. This prompted us to enquire into the ecological factors that may promote the use of marine resources during the breeding cycle. For this, during the 2014–2015 and 2015–2016 seasons, 400 regurgitated pellets were collected over the breeding season for different stages in the nesting cycle: incubation, early and late chick rearing. Prey items were classified according to different categories (penguin, fish, mollusk, and crustacea), and the occurrence frequency of each category was determined. As expected, penguins were the main prey consumed, but the occurrence of fish and mollusks increased for both early and late care of chicks. The flexibility in skua foraging behavior may be related to the changing degree of central place forager, and to the fluctuating energy requirements during each breeding stage. Moreover, the conspicuous decline in penguin availability or accessibility induced by intraspecific competition, may represent an alternative driving force in their foraging behavior over the breeding season.

**Keywords** Diet · Marine resources · Breeding · Brown Skua · *Stercorarius antarcticus* · Antarctica

## Introduction

Competition and prey availability represent ecological factors that may impact individual foraging behavior (Ratcliffe et al. 2018; Busdieker et al. 2019). Intra- and interspecific competition may constrain the accessibility and the apparent abundance of preferred prey which can result in diet variation at individual and population levels (Ratcliffe et al. 2018). When resources are abundant, animals consume a

reduced number of prey types which provide a high energy income. However, seasonal fluctuation in prey availability may force organisms to use alternative resources (Nelson 1980; Bolnick 2004). Therefore, this set of factors may induce an increase of the population niche width, diet divergence, and flexibility in foraging behavior (Terraube and Arroyo 2011).

Brown Skuas (*Stercorarius antarcticus*) are opportunistic predators and scavengers in both terrestrial and marine environments in Antarctic and sub-Antarctic locations (Ritz et al. 2008; Carneiro et al. 2015; Graña Grilli and Montalti 2015; Borghello et al. 2018). At breeding locations, skua diet is diverse and in Antarctic locations skua diet shows a significant reliance on penguins (Graña Grilli and Montalti 2015; Borghello et al. 2018). Skua diet has been studied during the reproductive period in areas with a variable degree of interspecific competition and resource availability (Furness 1987; Pietz 1987; Moncorps et al. 1998; Mougéot et al. 1998; Reinhardt et al. 2000; Anderson et al. 2009; Graña Grilli and Montalti 2012, 2015; Graña Grilli et al. 2014). When Brown Skuas breed

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in sympatry with other predators, such as the South Polar Skua (*Stercorarius maccormicki*), a partition of the feeding niche occurs (Malzof and Quintana 2008; Graña Grilli et al. 2011; Graña Grilli and Montalti 2012). In this circumstance, Brown Skuas monopolize terrestrial resources (i.e., penguins and other seabird eggs and chicks), while South Polar Skuas feed almost exclusively at sea (Trivelpiece et al. 1980; Graña Grilli and Montalti 2012). Moreover, at locations with no interspecific competition Brown Skuas seem to prefer terrestrial prey and contrary to common statements about their opportunistic behavior, studies have demonstrated that often skuas show preferences in prey selection (Reinhardt et al. 2000).

At Esperanza/Hope Bay, breeding Brown Skuas do not compete with other species such as South Polar Skuas, and coexist with a high number of non-breeding conspecifics (senescent, immature individuals, and failed breeders). Breeding skuas nest nearby a large breeding colony of over 100,000 breeding pairs of Adélie (*Pygoscelis adeliae*) and Gentoo (*Pygoscelis papua*) Penguins (Santos et al. 2018), which provide an important source of food for skuas. At this location, breeding skuas feed primarily on penguins and exhibited a higher consumption of marine prey (fish and invertebrates) compared to non-breeding skuas (Borghello et al. 2018). Furthermore, despite the high availability of terrestrial resources, the use of marine prey was higher than

that reported in other Antarctic locations (Borghello et al. 2018).

To gain further insight on Brown Skua feeding habits, we analyzed the qualitative contribution of marine resources during the reproductive period. For this, we addressed the use of marine prey in different breeding stages by analyzing prey items from regurgitated pellets.

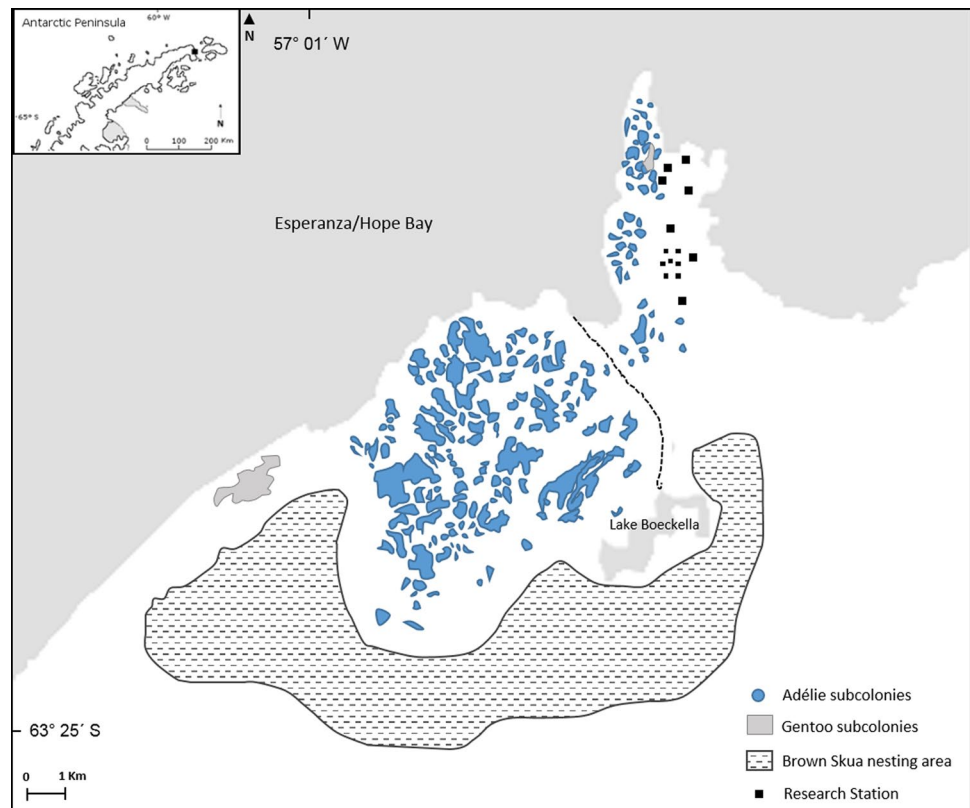
## Materials and methods

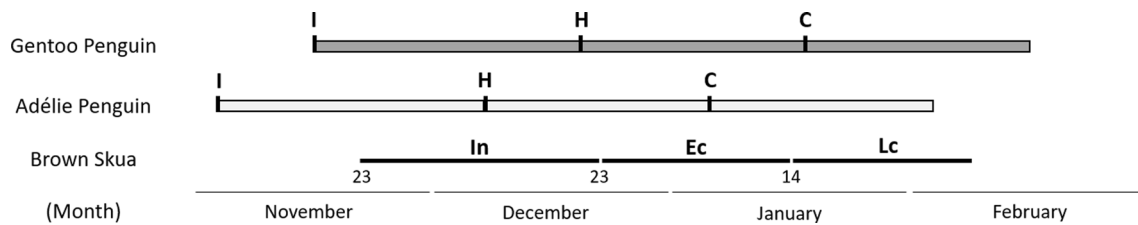
### Study site and sample collection

The study was conducted during the breeding seasons of 2014–2015 and 2015–2016 at Esperanza Bay, Antarctic Peninsula ( $63^{\circ} 24' S$ ,  $57^{\circ} 01' W$ ) (Fig. 1). Brown Skuas breed at this location from November to February (Coria and Montalti 1993). Based on counts of active nests, there were 19 breeding pairs of Brown Skuas present during 2014–2015 and 23 pairs during 2015–2016; at the same time a large colony of Adélie penguins and two smaller colonies of gentoo penguins existed nearby (Santos et al. 2018) (Fig. 2).

Upon our arrival to the study site, we cleared the area surrounding each nest of pellets to avoid the collection of samples belonging to previous seasons. These pellets were discarded, and we collected fresh pellets for analysis. For this study three reproductive stages were defined: egg

**Fig. 1** Map of the study area at Esperanza Bay, Antarctic Peninsula ( $63^{\circ} 24' S$ ,  $57^{\circ} 01' W$ ). Nest location of Brown Skuas (*Stercorarius antarcticus*) during the seasons 2014–2015 and 2015–2016. Also, the distribution of the Adélie (*Pygoscelis adeliae*) and gentoo (*Pygoscelis papua*) colonies are indicated





**Fig. 2** Breeding stages of Brown Skuas (*S. antarcticus*) and Adélie (*P. adeliae*) and Gentoo (*P. papua*) penguins at Esperanza (Hope) Bay. Numbers indicate the initial day for the incubation (In), early

(Er) and late (Lr) rearing stages for Brown Skuas. The breeding cycle of penguins was divided in three stages corresponding to *I* incubation, *H* hatching, and *C* crèche

incubation (In), early (Er) and late rearing (Lr) of chicks. For In, the sampling was performed during incubation of eggs (since 23 November). For Er, pellets were collected during 20 days after egg hatching (approximately, 23 December–14 January) and, for the Lr stage pellets were collected until chicks were completely feathered (about 40 days old; 15 January–6 February) (Fig. 2). Pellets were collected every five days, providing a total of 400 pellets over the two breeding seasons ( $n_{In} = 76$ ;  $n_{Er} = 150$  and  $n_{Lr} = 174$ ). During 2014–2015 we collected 120 pellets ( $n_{In} = 21$ ,  $n_{Er} = 46$  and  $n_{Lr} = 53$ ) and for 2015–2016 we collected 280 pellets from 12 nests ( $n_{In} = 55$ ,  $n_{Er} = 104$  and  $n_{Lr} = 121$ ). Comparative inter-annual analyses of the diet from each nest could not be assessed. In addition, as some nests failed during the incubation or during the early rearing of the chicks, it was not possible to collect pellets from all nests for all stages in breeding cycle. Once in the laboratory pellets were dried at room temperature, placed in nylon stockings, and stored in cardboard boxes until their analysis.

### Sample analysis, dietary item classification and identification

Each pellet was placed into a petri dish and disaggregated to separate contents. The material was sorted into prey items under a binocular microscope (4X). Pellet content was classified according to the following general prey categories: terrestrial (penguins) and marine (fish, mollusk [gastropods and cephalopods] and crustacea) with particular dietary items identified and classified into subcategories: penguins (feathers, chicks' bone remains, and egg shell), fish (otoliths, scales, crystalline, and fish vertebrae), and mollusks, (gastropod shell remains from limpets and cephalopod beaks; Xavier et al. 2018).

Otoliths were identified to species level by using specialized literature (Hetch 1987; Reid 1996). Otoliths were sorted into right and left with the higher number defining the number of fish present in the sample. Fish size was inferred from otolith size by measuring otolith longitudinal (OW) and vertical (OL) axes using a binocular microscope (16X);

total length (TL, mm) of fish was estimated by using the appropriate formula for each species (Hetch 1987).

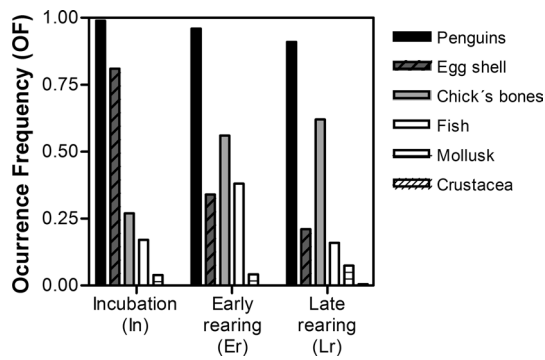
Results of the general prey categories and particular dietary items were expressed as occurrence frequency (OF), calculated by the formula  $OF = (f_i/N)$ , where  $f_i$  is the number of pellets with item  $i$  and  $N$  is the total number of pellets (De Villa Meza et al. 2002; Malzof and Quintana 2008). In a few cases, pellets contained more than one item from each category, such as otoliths and vertebrae for “fish category”, for example. In this situation the contribution to the NO value for the fish prey category was considered as 1.

### Statistical analysis

To test for differences in the consumption of food items between different breeding stages (In, Er and Lr) and between years (2014–2015 and 2015–2016) the chi-square ( $\chi^2$ ) test was performed. Values of  $\chi^2_{df}$ , where  $df$  = degree of freedom. To evaluate differences in total length (TL) of the fish consumed, a One-way ANOVA test was performed with values of  $F$  and  $p$  are described for each result. A difference with  $p < 0.05$  was considered significant.

### Results

Penguin consumption throughout the breeding season showed a decline toward the Lr stage ( $\chi^2 = 7.416$ ,  $p = 0.024$ ). During the In stage a higher OF of penguin egg shell (OF: 0.81) was observed ( $\chi^2 = 81.77$ ,  $p < 0.0001$ ) compared to the chick rearing stages (Er OF: 0.34; Lr OF: 0.21). Moreover, during the chick rearing stages a decrease in the use of penguin eggs was observed, whereas a significant increase in the OF of penguin chicks' bone remains occurred (Er OF: 0.56; Lr OF: 0.68) ( $\chi^2 = 36.73$ ,  $p < 0.0001$ ) (Fig. 3 and Table 1). These results reflect a switch in Brown Skua diet from penguin eggs to chicks between the In and Er stages. Despite penguins being a major component of skua diet throughout the entire breeding period, we focused our study on skua use of marine resources (Fig. 3 and Table 1). The total number of dietary items from marine prey found in pellets in each breeding stage was In = 17, Er = 63, and Lr = 33 (Table 1).



**Fig. 3** Occurrence frequency (OF) of dietary prey categories found in regurgitated pellets during the different breeding stages of Brown Skuas (*S. antarcticus*) ( $n=400$ ; In = 76, Er = 150, and Lr = 174). Prey categories are penguin, fish, mollusk, and crustacea. For penguin category, the OF of the particular dietary items egg shells and chick's bone remains were also represented

Fish consumption showed differences throughout the breeding period ( $\chi^2 = 8.911$ ,  $p = 0.0116$ ). The OF of the Fish category was higher during the Er stage (OF: 0.38) compared to In (OF: 0.17) and Lr (OF: 0.11) stages (Fig. 3).

The consumption of mollusk showed an increase toward the Lr stage but this was not statistically significant ( $\chi^2 = 2.303$ ,  $p = 0.3162$ ) (Fig. 3). During In and Er stages the OF was 0.04, and increased to 0.07 during the Lr stage. An increase in the prey item “limpets” was observed, while one Cephalopod beak was found toward the Lr stage (Table 1). Moreover, during the Lr stage one item corresponding to Crustacea category (Antarctic Krill, *Euphausia superba*) was found (Fig. 3).

Wilson's storm petrel (*Oceanites oceanicus*) bone remains were found only in two pellets during the season

**Table 1** Dietary prey items identified for each category in the regurgitated pellets of Brown Skuas (*S. antarcticus*) at Esperanza Bay, Antarctic Peninsula, during the different breeding stages (In, Er, and Lr)

Item/breeding stage	In ( $n=76$ )		Er ( $n=150$ )		Lc ( $n=174$ )	
	NO	FO	NO	FO	NO	FO
Penguins	75	0.99	144	0.96	158	0.91
Egg shell	62	0.81	51	0.34	38	0.21
Chicks bone remains	21	0.27	84	0.56	120	0.68
Fish	14	0.17	57	0.38	19	0.11
Vertebrae	11	0.14	47	0.31	14	0.08
Otoliths	2	0.03	9	0.06	6	0.03
Crystallines	0	0.00	0	0.00	1	0.01
Scales	1	0.01	1	0.01	4	0.02
Mollusk	3	0.04	6	0.04	13	0.07
Gastropod limpets	3	0.04	6	0.04	12	0.06
Cephalopods beaks	0	0.00	0	0.00	1	0.01
Crustacea	0	0.00	0	0.00	1	0.01
Krill	0	0.00	0	0.00	1	0.01

In a few cases, pellets contained more than one particular item from each category, such as otoliths and vertebrae for “fish category”, for example. In this particular situation the contribution to the NO value for the fish prey category was considered as 1. NO number of occurrence; OF occurrence frequency

**Table 2** Analysis of interannual differences in the use of land and marine prey

Season	Penguin						Fish						Mollusk					
	In		Er		Lr		In		Er		Lr		In		Er		Lr	
	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO
2014–2015	21	1	42	0.91	47	0.88	3	0.14	12	0.26	7	0.13	1	0.04	2	0.04	5	0.09
2015–2016	54	0.98	100	0.96	111	0.91	11	0.17	45	0.4	12	0.1	2	0.03	4	0.08	7	0.06
$\chi^2$	0.386		0.038		0.646		0.245		3.997		0.411		0.051		0.021		0.764	
$p$	0.533		0.843		0.421		0.623		0.045*		0.521		0.821		0.885		0.382	

Dietary items recorded in the regurgitated pellets of breeding Brown Skuas (*S. antarcticus*) were compared between years (2014–2015 and 2015–2016) for each stage (incubation, early and late rearing of chicks). The occurrence frequency (OF) and the number of occurrence (NO) are reported. Values of chi-squared ( $\chi^2$ ), degree of freedom (df) = 2 and  $p$  are reported

\* $p < 0.05$

2015–2016. This indicates that flying seabirds have a minor contribution to the diet of Brown Skuas.

Most prey categories, did not show interannual differences for each breeding stage (Table 2), though during the Er stage the OF of Fish was higher during the season 2015–2016 ( $\chi^2 = 3.997$ ,  $p = 0.045$ ).

A total of 17 fish otoliths were recovered ( $n_{In} = 2$ ;  $n_{Er} = 9$  and  $n_{Lr} = 6$ ). Two fish species were identified Antarctic silverfish (*Pleuragramma antarcticum*) and Antarctic lanternfish (*Electrona antarctica*). The most frequent was *P. antarcticum*, present in 14 pellets. To evaluate associations between the size of the fish consumed and the breeding stage, the total length of *P. antarcticum* was estimated as  $TL = 99.6 \times OL^{1.05}$  and for *E. antarctica*  $TL = 31.42 \times OL^{1.109}$ . No differences were observed in total length of *P. antarcticum* through the breeding stages (TL: ANOVA,  $F = 1.047$ ,  $p = 0.3836$ ) (Fig. 4). For *E. antarctica* the TL was  $96.82 \pm 2.70$  mm.

Among mollusks, gastropods were the most abundant in the diet of Brown Skuas. Limpets and shell remains revealed that *Nacella concinna* was consumed by breeding skuas. Cephalopod species could not be precisely identified based on beak characteristics and morphology because remains were eroded. Nevertheless, the analysis of these remains indicated that they belonged to Psychroteuthidae or Cranchiidae, cephalopod families well represented in the Antarctic region.

## Discussion

Brown Skuas consume a broad diversity of prey and their diets are often demarcated by the breeding phenology of their prey (Moncorps et al. 1998; Reinhardt 2000; Phillips et al. 2004; Graña Grilli and Montalti 2015). At Esperanza Bay, Brown Skuas breed near a colony of Adélie and Gentoo penguins (Santos et al. 2018) which skuas successfully exploit as a food source as their main prey type. There is, however, a significant contribution of marine prey to Brown Skua diet (Borghello et al. 2018).

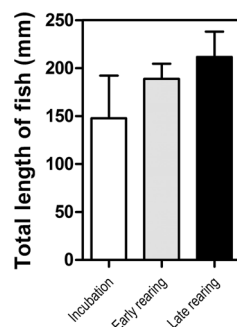
Analysis of regurgitated pellets is a useful method to determine seabirds' diet. This approach provides information on the relative importance of different prey (Barret et al. 2007). However, this method is biased because it overestimates prey items that are swallowed whole or composed of hard parts, it underestimates items composed of soft tissue, and it does not allow for an accurate determination of the biomass consumed (Votier et al. 2003).

Seabirds need to balance different energy demands during breeding (Weimerskirch and Lys 2000; McLeay et al. 2010), and therefore adapt their foraging behavior (Navarro et al. 2009; Hipfner et al. 2013). Egg incubation and rearing of chicks imply great energy expenditure (Weimerskirch and Lys 2000). During these stages of breeding, it is expected that major shifts in diet and foraging strategies may occur (Hedd et al. 2014; Quillfeldt et al. 2014). In our study, we showed that during incubation Brown Skuas rely on penguin eggs and when skuas are rearing their chicks there is an increase in the consumption of penguin chicks and marine prey (fish and mollusk). This variation in diet composition reflects the flexibility of skua foraging strategy by supplementing the food obtained on land by traveling to the ocean (Carneiro et al. 2014, 2015; Graña Grilli et al. 2014).

The fish species we found were two notothenioids—*P. antarcticum* and *E. antarctica*—which have also been recorded in Brown Skua diet from other Antarctic locations (Malzof and Quintana 2008; Graña Grilli and Montalti 2012). During the Antarctic spring and summer seasons an increase in the abundance of both juvenile and adult notothenioids occurs at this latitude of the Peninsula (Kellermann 1986; Hubold and Tomo 1989; Caccavo et al. 2018). Based on otolith size, there were no significant differences in fish TL. Variations in fish TL may be related to both developmental stage of the fish, or, to differences in the foraging distances by skuas. However, it is not possible to infer whether skuas are selecting fish based on their size. To confirm skua prey selection strategies would require focal observations in future studies.

The quality of the resources consumed by parents has direct consequences on breeding success (Davoren and Burger 1999). Feeding on rich energy prey may improve breeding fitness and chick's quality (Van Donk et al. 2017). Usually, parents feed themselves and their chicks with a high-quality diet, for instance, with lipid-rich fish (Wilson et al. 2004; Bugge et al. 2011; Dänhardt et al. 2011; Mack-Ley et al. 2011; Isaksson et al. 2016) which provide a high antioxidant lipid content to prevent oxidative damage (Reinhardt and Van Vleet 1986; Surai et al. 2001). Fish consumption by skuas increased during the intensive care of chicks (Er), whereas a decline in fish consumption toward the late care (Lr) was observed. A possible explanation is that during the Lr stage Brown Skuas consume fewer but larger fish. Alternatively, another fish source could be the secondary intake from stomach contents of dead penguins. During

**Fig. 4** Size of fish found in regurgitated pellets from Brown Skuas (*S. antarcticus*) through the breeding stages (incubation, early and late rearing of chicks). Data represent the mean  $\pm$  SD of TL (mm) calculated for *Pleuragramma antarcticum* using the formula  $TL = 99.6 \times OL^{1.05}$  (Hetch 1987)



reproduction, the changing requirements in terms of prey energy content in adults and chicks may also induce flexibility in the feeding habits. The interannual differences in fish consumption may reflect an underestimation of this prey during the season 2014–2015 as a result of the sampling design, and not to a seasonal decline in fish availability.

Dietary supplementation with marine resources may be often related to an increase in the abundance of marine prey (krill and fish) or, to variations in land prey availability (Reinhardt 2000). At Esperanza Bay, Santos et al. (2018) reported a decline of 15.9% in the Adélie penguin population during the last 27 years. During this long period no studies were conducted on Brown Skua populations except for a report of 7 breeding pairs by Montalti and Coria (1993). During the 2014–2015 and 2015–2016 seasons we reported 19 and 23 breeding pairs, respectively, which were present among a larger number of non-breeding skuas ( $n = 64$  to 83 individuals) (Borghello et al. 2018). The decline in Adélie penguin population, and the increase of Brown Skua population, may have influenced the apparent availability of land resources forcing skuas to feed on the ocean. Alternatively, as was suggested by Votier et al. (2007) in increasing skuas' populations, a density-dependent effect may occur with an increase in fish consumption, apparently due to a competitive interaction with conspecifics for land prey.

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 offer a potential food source to predators. Nevertheless, these areas also represent a challenge and an energy cost of foraging for predators, because prey display effective defense strategies (Halupka and Halupka 1996; Busdieker et al. 2019). Here, we observed that Brown Skua diet composition depends on the breeding phenology of penguins (Fig. 2). During incubation skuas feed on penguin eggs and when rearing chicks, skuas shift to feeding on penguin chicks as has been reported in previous studies (Graña Grilli and Montalti 2015). The increase in the consumption of marine prey may be related to effective defense of their chicks by adult penguins which may force skuas to supplement their diet with marine prey.

When Brown and South Polar skuas breed in sympatry, competition and exclusion from feeding territories occurs. Brown Skuas monopolize terrestrial resources, and South Polar Skuas feed on marine resources (Trivelpiece and Volkman 1982; Young 1994; Malzof and Quintana 2008; Graña Grilli and Montalti 2015). This behavior may also be constrained by the availability of resources (i.e., penguin colony size) (Malzof and Quintana 2008). At Esperanza Bay, there is a high ratio of Brown Skuas to penguins ( $> 1:2000$ ) compared with other Antarctic locations: King George Island (1:230) (Carlini et al. 2009), Half Moon Island (1:1100) (Montalti et al. 2009), Deception Island (1:454) (Graña Grilli and Montalti 2012), and Cierva Point

(1:40) (Malzof and Quintana 2008). In contrast to these other Antarctic locations, interspecific competition at Esperanza Bay is very low. Only four South Polar Skuas pairs bred at Esperanza Bay with little overlap with Brown Skuas. Brown Skua pairs begin their incubation stage during November–January while South Polar Skuas begin in mid-January (*Ibañez unpublished data*). At this location prey density and interspecific competition may not constitute a driving force of variation in Brown Skuas' foraging behavior.

Individual dietary specialization may reduce the constraining effect of intraspecific competition by inducing ecological segregation (Patrick and Weimerskirch 2014; Ceia and Ramos 2015). At Esperanza Bay the degree of intraspecific competition seems to be high, since the number of non-breeding skuas gradually increase throughout the season. The non-breeder group reaches a maximum density when breeders are rearing their chicks. The feeding niche of breeders and non-breeders is completely overlap and both groups coexist sharing the same resources but using them differently (Borghello et al. 2018). The interaction between these groups may possibly limit the accessibility and availability of penguins, forcing breeders to forage in the ocean. Because of a limitation in our sampling design, inter-annual consistency in skua diet could not be addressed. As sampled individuals were possibly the same between seasons, and that skuas often display specialist feeding behavior (Anderson et al. 2009), data from each season cannot be considered independent. Hence, dietary specialization, as well as, inter-annual differences in resource availability could not be addressed. We acknowledge that this issue must be considered in future studies for a more detailed understanding on skua foraging behavior.

Our results suggest that Brown Skua feeding habits during breeding are conditioned by a variety of complex and interacting factors. Prey phenology and the competitive exclusion by conspecifics may be relevant drivers of flexibility in their foraging strategy. The flexibility observed in skua diet may represent only a minor component within the complex behavioral and physiological adaptations skuas follow in fulfilling the energy requirements of growing chicks and self-maintenance.

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**Author contributions** AEI contributed during fieldwork, sample analysis, analysis of the results, and writing the manuscript. PB and LMM

contributed with the sample analysis. DST contributed during the fieldwork and sample analysis. DM contributed with sample analysis and writing the manuscript. All authors read and approved the manuscript.

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## Declarations

**Conflict of interest** The authors declare no conflict of interests.

**Ethical approval** The permit to carry out the fieldwork for this work was evaluated and provided by the Ethics Committee of the Environment Office from the Dirección Nacional del Antártico (DNA). All applicable international, national, and institutional guidelines for sampling, care and experimental use of animals for the study were followed as established by the Article III, Annex II of the Madrid Protocol, Law 24.216 (Taking, Harmful Intrusion and Introduction of Species) within the framework of the projects evaluated by the Instituto Antártico Argentino (IAA) and Dirección Nacional del Antártico (DNA).

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