ORIGINAL PAPER

Diet of the south polar skua *Catharacta maccormicki* and the brown skua *C. antarctica lonnbergi* at Cierva Point, Antarctic Peninsula

Silvina L. Malzof · Rubén D. Quintana

Received: 19 November 2007/Revised: 15 January 2008/Accepted: 21 January 2008/Published online: 3 April 2008 © Springer-Verlag 2008

Abstract South polar skuas, SPS, (Catharacta maccormicki) and brown skuas, BS, (C. antarctica lonnbergi) are regarded as opportunistic predators. When breeding in sympatry, BS feed mainly on penguin eggs and chicks, while SPS forage almost exclusively at sea. The objective of this study was to determine the diet composition of adult SPS and BS breeding in sympatry, in order to assess food resource partitioning between these species. The total number of food items consumed was 375 for BS and 682 for SPS in 1992-93, and 427 for BS and 579 for SPS in 1995-96. The pellets composition was significantly correlated between skua species for the same breeding season $(r_{\rm s} = 0.67, p = 0.0062 \text{ and } r_{\rm s} = 0.81, p < 0.001, \text{ for}$ 1992-93 and 1995-96, respectively), and between breeding seasons for the same skua species ($r_s = 0.71$, p = 0.001and $r_s = 0.81$, p < 0.001, for SPS and BS, respectively). Trophic niche breadth of BS was wider than that of SPS $(B_{A(BS)} = 0.28 \text{ and } B_{A(SPS)} = 0.24; Z = 7.67; p < 0.001).$ The trophic niche overlap between BS and SPS was over 65% in both breeding seasons. In agreement with other studies on the diet of these skua species in situations of sympatry, SPS consumed more fish and BS consumed more birds.

S. L. Malzof · R. D. Quintana (⊠)
Laboratorio de Ecología Regional,
Dpto. de Ecología, Genética y Evolución,
FCEyN, Universidad de Buenos Aires,
Pabellón II, Ciudad Universitaria,
1428 Buenos Aires, Argentina
e-mail: rubenq@ege.fcen.uba.ar

R. D. Quintana

National Scientific and Technical Council (CONICET), Buenos Aires, Argentina **Keywords** Antarctic Peninsula · Brown skua · Diet composition · Sympatric breeding · South polar skua · Trophic niche breadth · Trophic niche overlap

Introduction

Skuas of the genera *Catharacta* and *Stercorarius* have remarkably diversified diets in different localities where they breed (see reviews in Furness 1987). The most common Antarctic skua species, the south polar skua, SPS (*Catharacta maccormicki*) and the brown skua, BS (*C. antarctica lonnbergi*), are regarded as opportunistic predators, scavengers and kleptoparasites, on a wide variety of organisms (e.g., Eklund 1961; Müller-Schwarze and Müller-Schwarze 1977; Moors 1980; Maxon and Bernstein 1982; Osborne 1985; Green 1986; Pietz 1987; Norman and Ward 1990; Young 1990; Zipan and Norman 1993; Norman et al. 1994). During the reproductive period, they may feed on terrestrial resources (Furness 1987) and despite their opportunism, they depend primarily on a few prey types (Pietz 1987).

Although these skua species usually breed in disjunct areas, they nest sympatrically in a hybrid zone at the Antarctic Peninsula, between 61 and 65°S (Pietz 1987; Ritz et al. 2006). When breeding in sympatry, some authors have stated that BS feeds mainly on penguin eggs and chicks, while SPS forages almost exclusively at sea (Parmelee et al. 1978; Trivelpiece et al. 1980; Hemmings 1984; Pietz 1987; Peter et al. 1990). However, other studies have shown that the feeding habits of skuas and the selection of their breeding areas are largely dependent on penguin rookeries in combination with food availability at sea (Young 1963; Müller-Schwarze and Müller-Schwarze 1973; Trillmich 1978; Hull et al. 1994). The objective of the present study was to determine the diet composition of adult SPS and BS breeding in sympatry at Cierva Point, Antarctic Peninsula, in order to assess food resource partitioning between these species.

Materials and methods

The study was carried out during the austral summers (from December to February) of 1992–93 and 1995–96 at Cierva Point, Danco Coast, on the west side of the Antarctic Peninsula, between Gerlache Strait and Cierva Cove ($64^{\circ}09'S$, $60^{\circ}57'W$). This location is composed of a heterogeneous mosaic of different habitat types in a relatively small area (c. 3 km²). General geomorphological features and the particular climatic conditions provide a variety of microhabitats and shelters for birds (Agraz et al. 1994).

The area supports a high-avian diversity including two small colonies of gentoo (*Pygoscelis papua*) and chinstrap (*P. antarctica*) penguins (Quintana et al. 2000). Important sympatric breeding colonies of SPS and BS were observed during the studied periods. In 1995–96, for example, the total number of breeding pairs of both skua species was 182 (93 SPS, 26 BS, eight mixed pairs and 55 pairs not classified; Quintana et al. 2000).

A total of 212 (56 from BS and 156 from SPS) and 201 (92 from BS and 109 from SPS) regurgitated pellets were collected during the breeding seasons of 1992–93 and 1995–96, respectively. All the pellets were collected fresh (still wet inside), in the proximity of nests of those breeding pairs that could be identified as SPS or BS. Identification of skua species was made by reference to morphological features and plumage colours. Sample design followed the outlines of Design #1 stated by Thomas and Taylor (1990).

Pellets were dried at room temperature, placed in nylon stockings and stored in cardboard boxes for their transportation to Argentina. Once in the laboratory, each pellet was placed into a petri dish and disaggregated in 75% EtOH to separate contents, which were classified according to the following food item categories: remains of chicks and adult birds (bone fragments and feathers), eggshell fragments, and fish remains (otoliths, scales and bone fragments). Other pellet components, such as vegetation, pebbles, refuse, seashells and arthropods were also identified.

Most of the fish otoliths were identified to species level by comparisons with reference material at the Museo Argentino de Ciencias Naturales "B. Rivadavia" (MACN), and using specialized literature (Hetch 1987; Williams and McEldowney 1990; Reid 1996). The otoliths belonging to specimens of each species were sorted into right or left in order to estimate the number of fish per sample. Otolith length and width were measured to the nearest 0.01 mm and the size of each fish species was determined using the equations proposed by Hetch (1987) and Reid (1996). The length of *Pagetopsis* sp. was calculated with the formula used for a related species (*Chaenodraco wilsoni*), while that of *Trematomus* sp. was calculated with the formula for *T. newnesi* (Hetch 1987).

Results were expressed as frequency of occurrence (FO), which was calculated by the formula FO = (f_i/N) , where f_i is the number of pellets with item *i* and *N* is the total number of pellets. Relative frequency of food items RF = $(f_i/\Sigma f_i)$ was estimated as the number of times food item *i* was found as a percentage of all food items found. Although FO indicates, how common an item is in the pellets, RF provides a better indication for how often an item is consumed because it accounts for multiple items being found in a pellet (De Villa Meza et al. 2002). Consequently, RF data were used for the subsequent analysis.

The two-tailed Spearman rank correlation coefficient (Zar 1996) was used for comparisons of the diets between breeding seasons for each skua species and between skua species for the same breeding season. The χ^2 test (Siegel and Castellán 1988) was performed to test for differences in the consumption of the main food items between breeding seasons for each skua species and between skua species for the same breeding season. The two species showed a high frequency of pellets with skua remains. This fact could result in an increased similarity of their diets, and therefore both analyses were repeated after the removal of pellets containing skua remains.

The trophic niche breadth was calculated with the standardized Levins' index, B_A (Hurlbert 1978; Krebs 1999), using the average data from the two breeding seasons. A bootstrap technique was used to estimate niche breadth values and their associated variances (Jaksic and Medel 1987). Differences in niche breadth between skua species were assessed using a Mann–Whitney normal approximation test (Zar 1996). Finally, the percentage overlap index (Krebs 1999) was used to evaluate the overall niche overlap between BS and SPS.

Results

The total number of items consumed was 375 for BS and 682 for SPS in the breeding season 1992–93, and 427 for BS and 579 for SPS in the breeding season 1995–96 (Table 1). Pellets contained not only animal remains but also vegetation (mainly mosses), pebbles, and, to a lesser extent, refuse from the Antarctic station "Primavera" (Table 1). The moss *Polytrichum alpestre* was the only item found in 32 pellets of SPS and nine pellets of BS for 1992–93, and in nine pellets of SPS and two of BS for 1995–96.

 Table 1
 Food item categories recorded in the regurgitated pellets of brown skua (BS) and south polar skua (SPS) at Cierva Point, Antarctic Peninsula, for the breeding seasons 1992–93 and 1995–96

Food items	BS 1992–93 (<i>N</i> = 56)		SPS 1992–93 (N = 156)			BS 1995–96 (<i>N</i> = 92)			SPS 1995–96 (<i>N</i> = 109)			
	NO	FO	RF	NO	FO	RF	NO	FO	RF	NO	FO	RF
Penguin	30	0.08	0.23	47	0.07	0.15	87	0.20	0.38	33	0.06	0.11
Adult	13	0.23	0.10	18	0.12	0.06	19	0.21	0.08	9	0.08	0.03
Chick	13	0.23	0.10	18	0.12	0.06	59	0.64	0.25	19	0.17	0.07
Eggshell	4	0.07	0.03	11	0.07	0.03	9	0.10	0.04	5	0.05	0.02
Skua	19	0.05	0.15	44	0.06	0.14	9	0.02	0.04	53	0.09	0.18
Adult	12	0.21	0.09	20	0.13	0.06	3	0.03	0.01	21	0.19	0.07
Chick	5	0.09	0.04	9	0.06	0.03	5	0.05	0.02	28	0.26	0.10
Eggshell	2	0.04	0.02	15	0.10	0.05	1	0.01	0.00	4	0.04	0.01
Storm Wilsońs petrel (adult)	1	0.02	0.01	4	0.03	0.01	0	0.00	0.00	0	0.00	0.00
Antarctic tern (adult)	0	0.00	0.00	0	0.00	0.00	1	0.01	0.00	0	0.00	0.00
Unidentified birds	6	0.11	0.05	6	0.04	0.02	1	0.01	0.00	0	0.00	0.00
Total birds	56	0.15	0.43	101	0.15	0.31	98	0.23	0.42	86	0.15	0.30
Fishes	69	0.18	0.53	208	0.30	0.65	133	0.31	0.57	202	0.35	0.70
Electrona Antarctica	33	0.59	0.25	115	0.74	0.36	87	0.95	0.38	131	1.20	0.45
Pleurogramma antarcticum	9	0.16	0.07	9	0.06	0.03	2	0.02	0.01	15	0.14	0.05
Protomyctophum choriodon	18	0.32	0.14	21	0.13	0.07	22	0.24	0.09	32	0.29	0.11
Trematomus sp.	4	0.07	0.03	0	0.00	0.00	6	0.07	0.03	4	0.04	0.01
Gymnoscopelus nicholsi	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	1	0.01	0.00
Protomyctophum tenisoni	0	0.00	0.00	0	0.00	0.00	1	0.01	0.00	1	0.01	0.00
Pagetopsis sp.	0	0.00	0.00	0	0.00	0.00	1	0.01	0.00	2	0.02	0.01
Unidentified fishes	5	0.09	0.04	63	0.40	0.20	14	0.15	0.06	16	0.15	0.06
Invertebrate	3	0.05	0.02	10	0.06	0.03	1	0.01	0.00	0	0.00	0.00
Seashells	2	0.04	0.02	2	0.01	0.01	0	0.00	0.00	1	0.01	0.00
Vegetation												
Polytrichum alpestre	56	1.00		116	0.74		64	0.70		102	0.94	
Other Mosses	8	0.14		15	0.10		19	0.21		62	0.57	
Deschampsia antarctica	10	0.18		10	0.06		12	0.13		7	0.06	
Lichens	9	0.16		25	0.16		20	0.22		60	0.55	
Prasciola crispa	3	0.05		16	0.10		0	0.00		0	0.00	
Pebbles	158	2.82		159	1.02		76	0.83		55	0.50	
Refuse	1	0.02		20	0.13		4	0.04		4	0.04	

t Antere

829

N number of analysed pellets, NO number of occurrences, FO frequency of occurrence, RF relative frequency

The composition of regurgitated pellets was significantly correlated between skua species for the same breeding season ($r_s = 0.67$, n = 15, p = 0.0062 and $r_s = 0.81$, n = 18, p < 0.001, for 1992–93 and 1995–96, respectively), and between breeding seasons for the same skua species ($r_s = 0.71$, n = 18, p = 0.001 and $r_s = 0.81$, n = 18, p < 0.001, for SPS and BS, respectively).

After the removal of the pellets with skua remains, both species still showed a high correlation between their diet composition in 1992–93 ($r_s = 0.83$, n = 8, p = 0.01), whereas this was not the case in 1995–96 ($r_s = 0.09$, n = 9, p = 0.83). The diet composition of each species between the two reproductive seasons correlated in BS

 $(r_{\rm s} = 0.73, n = 9, p = 0.03)$ but not in SPS $(r_{\rm s} = 0.20, n = 9, p = 0.60)$.

In both breeding seasons, SPS consumed more fish and BS consumed more birds (Tables 1, 2). When the diets of SPS and BS were compared for the same breeding season, there was a significant difference in the occurrence of fish, penguin, and total birds. In contrast, when the diets of SPS and BS were compared between the two breeding seasons, they only differed significantly in the occurrence of penguin in BS diets (Table 2a, b). The removal of the pellets containing skua remains showed significant differences in the diets of SPS and BS only in 1995–96. Likewise, the occurrences of fish, penguin, and total birds differed

Table 2 Comparison of the relative frequency of fish.		Between species				Between season					
penguin, and birds (including		1992–93	1992–93		1995–96		SPS				
penguins) with respect to the remaining food items, between		χ^2	Р	χ^2	Р	χ^2	Р	χ^2	Р		
skua species for the same breeding season and between breeding seasons for each skua species	Considering all analysed pellets										
	Fish	4.88*	0.03	8.32*	< 0.01	1.57	0.21	1.53	0.22		
	Penguin	4.07*	0.04	47.92*	< 0.01	1.12	0.29	46.9	< 0.01*		
	Total birds	5.00*	0.03	8.24*	< 0.01	0.14	0.71	0.001	0.97		
	After removal of pellets with skuas remains										
	Fish	0.37	0.54	45.85*	< 0.01	2.22	0.14	9.22	< 0.01*		
	Penguin	0.06	0.81	45.85*	< 0.01	14.80	< 0.01*	9.22	< 0.01*		
	Total birds	0.37	0.54	45.85*	< 0.01	18.71	0.14	4.07	0.04*		

* Significant differences

significantly between breeding seasons for BS, whereas penguin content was the only food item differing significantly in the diets of SPS (Table 2c, d).

Niche breadth of BS was wider than that of SPS $(B_{A(BS)} = 0.28 \text{ and } B_{A(SPS)} = 0.24; \text{ Mann-Whitney Z test:} Z = 7.67, n = 50, p < 0.001$). The trophic niche overlap between BS and SPS was 69.0% in the breeding season 1992–93 and 65.3% in the breeding season 1995–96.

We recovered 313 fish otoliths (215 from SPS and 98 from BS pellets) and 463 fish otoliths (296 from SPS and 167 from BS pellets) during the breeding seasons of 1992–93 and 1995–96, respectively. Seven fish species were identified (Table 1), of which, the most frequent was *Electrona antarctica*, followed by *Protomyctophum choriodon* and *Pleuragramma antarcticum*. Tables 3 and 4 show the length and width of otoliths and the estimated size of fishes consumed by the two skua species during the studied breeding seasons. For the breeding season 1992–93, the size of consumed fishes was 8.57–28.59 cm for BS and 6.43–30.50 cm for SPS, while during 1995–96, this range was 6.43–21.22 cm for BS and 4.72–18.31 for SPS (Table 4).

Discussion and conclusions

Using regurgitated pellets is a commonly used method for determining the diet of seabirds (Furness and Hislop 1981; Duffy and Jackson 1986; Green 1986; Norman and Ward 1990; Young 1990; Casaux and Barrera-Oro 1993; Mund and Miller 1995; Jahncke and Rivas 1998; Moncorsps et al. 1998; Favero et al. 2000; Kubetzki and Garthe 2003; Votier et al. 2001; 2003, 2004a). According to Votier et al. (2003), regurgitated pellets are cast in large numbers, can be collected with limited disturbance and generally easy to classify to prey type. In the present study, regurgitated pellets were used to analyse the feeding habits of sympatric SPS and BS. This method not only offered a fast and easy

way to obtain material for further analysis, but also allowed to identify the consumed fish species by otolith examination, because of their low degree of erosion. It should be noted that there is no general consensus on the effectiveness of regurgitated pellets in determining the diet composition of seabirds. Some authors consider that this method provides accurate information (Mund and Miller 1995; Jahncke and Rivas 1998), but others argue that it can lead to misleading results because of differential digestibility of food items or underestimation of soft prey items such as fish or carrion flesh (Duffy and Jackson 1986; Young 1990; Schulz and Gales 2004). On the other hand, Votier et al. (2003) have pointed out that regurgitated pellets may provide the best index of relative importance of prey types among time periods or localities, but caution that they do not provide the best absolute measure of diet composition. According to Carss et al. (1997) and Barrett et al. (2007), pellet analysis is better used for determining diet composition than for quantification of consumption due to several biases (e.g., variation in number of pellets produced by day, variation in proportion of otolith recovered, absence of hard parts of small prey in the pellets, etc.). However, the other sampling techniques also have many limitations (Gales 1985; Jackson and Ryan 1986; Jackson et al. 1987; Mund and Miller 1995; Votier et al. 2003).

Summarizing, as was pointed out by some authors (Mund and Miller 1995; Votier et al. 2003), the use of regurgitated pellets is a valuable method to analyse the diet of skuas, especially in studies like this one, which includes comparisons between species and reproductive seasons. However, it should be noted that the used method could have underestimated penguin consumption because skuas usually feed only on muscle and other soft body parts of penguin chicks, and pellets contain only indigestible material (Votier et al. 2003).

The composition of regurgitated pellets of BS and SPS, was similar for both skua species in each breeding season

Table 3Fish species identifiedfrom otoliths in regurgitatedpellets of brown and south polarskuas at Cierva Point, AntarcticPeninsula, during the breedingseason 1992–93 and 1995–96

Fish species	N	N	N	Length			Width		
	(right)	(left)	(Und) ^a	\overline{X} (mm)	SD	Size range (mm)	\overline{X} (mm)	SD	Size range (mm)
Brown skua									
1992–93									
Electrona antarctica	20	27	6	2.8	0.8	2.0-5.5	2.4	1.3	1.6–5.0
Pleuragramma antarcticum	11	3	0	2.2	0.8	2.0-3.5	2.1	0.9	1.6–3.5
Protomyctophum choriodon	14	12	1	2.9	1.0	2.1-5.3	2.3	0.7	1.6-4.0
Trematomus sp.	1	1	2	2.5	1.9	1.2-3.8	2.1	1.3	1.2-3.0
1995–96									
Electrona antarctica	65	59	2	2.5	0.5	1.5-3.8	2.0	0.3	1.3-2.8
Pleuragramma antarcticum	1	2	1	1.8	0.3	1.5-2.0	1.8	0.3	1.5-2.0
Protomyctophum choriodon	13	13	0	3.2	0.6	2.0-3.8	2.4	0.3	2.0-2.8
Trematomus sp.	6	2	0	1.7	1.0	1.1-3.0	1.4	0.6	1.1-3.0
Protomyctophum tenisoni	0	1	0	2.5	_	_	2.0	_	_
Pagetopsis sp.	0	0	1	1.3	_	_	1.3	_	_
South polar skua									
1992–93									
Electrona Antarctica	83	87	6	2.7	0.8	1.5-5.5	2.1	0.6	1.1-4.2
Pleuragramma antarcticum	7	5	0	2.1	0.7	1.1-3.8	2.0	0.8	1.1-3.5
Protomyctophum choriodon	15	7	1	3.8	1.4	2.0-5.8	3.0	1.1	1.6-4.4
Trematomus sp.	2	1	1	1.9	1.5	1.3-3.2	1.5	0.8	1.1-2.5
1995–96									
Electrona Antarctica	122	104	10	2.8	0.5	1.1-3.8	2.2	0.4	1.0-2.8
Pleuragramma antarcticum	8	5	0	1.9	0.3	1.0-2.0	1.9	0.3	1.0-2.0
Protomyctophum choriodon	21	18	0	3.4	0.6	2.1-3.8	2.5	0.3	1.8-3.0
Trematomus sp.	1	0	3	2.0	0.9	1.1-2.5	2.0	0.9	1.1-2.5
Gymnoscopelus nicholsi	1	0	0	7.0	_	_	_	4.0	_
Protomyctophum tenisoni	0	0	0	_	_	_	_	_	_
Pagetopsis sp.	1	0	1	1.0	0.3	0.8-1.2	1.0	0.3	0.8-1.2

N otolith number, \overline{X} total mean of otolith length and width, SDstandard deviation and size range, *Und* unidentified otoliths

^a Eroded or broken

Table 4 Species and size of fishes (SL) consumed by brown skua (BS) and south polar skua (SPS) at Cierva Point, Antarctic Peninsula, during the breeding seasons 1992–93 and 1995–96 based on otolith length using the equations proposed by Hetch (1987) and Reid (1996)

Fish species	Equation	BS			SPS			
		Fish siz range (æ cm)	Median size (cm)	Fish size range (cm)		Median size (cm)	
Electrona antarctica	SL = 42.69686 OL + 0.278033	6.4	23.3	13.5	2.8	26.3	13.9	
Pleuragramma antarcticum	SL = 76.67621 OL + 17.5014	13.3	28.6	18.6	9.4	30.5	17.1	
Protomyctophum choriodon	SL = 53.753 OL - 21.95	8.6	26.3	12.1	8.6	28.7	15.3	
Trematomus sp.	$SL = 58.14674 \text{ OL} + 37.74691^{a}$	10.2	25.9	10.8	10.2	21.2	12.5	
Gymnoscopelus nicholsi	SL = 28.61827 OL - 20.7910	-	-	_	18.0	_	-	
Protomyctophum tenisoni	SL = (OL - 0.416) / 0.0222	9.4	-	_	_	_	-	
Pagetopsis sp.	$SL = 63.92876 OL + 5.743653^{b}$	8.9	-	-	5.7	8.3	-	

Fish size range was obtained considering the minimun and maximun length of otoliths from each fish species

OL otolith length

^a Based on Trematomus newnesi

^b Based on Chaenodraco wilsoni

and for each skua species between the two breeding seasons. This fact is also reflected in the relatively high trophic niche overlap between skua species (>65%) in both breeding seasons. For the breeding season 1995–96, there were differences in the diet composition between the two skua species after the removal of pellets with skua remains; the observed differences were due to differential consumption of penguins, as indicated by the significant decrease in their frequency of occurrence in SPS pellets. The low penguin consumption in 1995-96 also resulted in the significant differences found for SPS between seasons. In the remaining comparisons, SPS consumed more fish and BS consumed more birds in general and penguins in particular. In this sense, a segregation in resource use was observed in the studied locality, in agreement with that proposed by other authors for cases, in which, BS and SPS live in sympatry (Parmelee et al. 1978; Trivelpiece et al. 1980; Hemmings 1984; Pietz 1987; Peter et al. 1990), even when the method used might have underestimated penguin consumption. In the South Shetlands and Orkney Islands, Raya Rey and Montalti (2000) pointed out that both skua species consumed a similar proportion of penguin and fish. However, in the present paper, the main prey consumed by BS and SPS was fish, while in that of Raya Rey and Montalti (2000), it was penguin. In this regard, our results differed from those of Pietz (1987), who stated that both studied skua species prefer to feed on penguins. Furthermore, some authors have observed that SPS defend penguin colonies as feeding territories in the absence of BS (Trillmich 1978; Young 1963; Müller-Schwarze and Müller-Schwarze 1973).

Taking into account that the breeding colony sizes of BS and SPS at Cierva Point, the abundance of skuas in this area might have led to an increased demand for food. Penguins usually provide a spatially and temporally predictable food supply for skuas, while availability of marine food sources is affected by the skuas' ability to gain access to them (Pietz 1987; Reinhardt et al. 2000). In addition, penguin chicks represent a better food resource for skuas because of the greater biomass and energy content (more than double) compared to fish species (Norman et al. 1994; Votier et al. 2004b). The important contribution of fish to the diet of BS and SPS observed in the present study could be due to the small size of the penguin colonies at Cierva Point (e.g., the Gentoo Penguin colony comprised only 890 and 1,041 breeding pairs for the breeding seasons 1992-93 and 1995-96, respectively; Quintana et al. 2000). This is in contrast to other Antarctic localities where penguin colonies with thousands of breeding pairs are available for skuas (Favero et al. 1991; Young 1994; Emslie et al. 1995; Coria et al. 1996; Bó and Copello 2001; Montalti and Soave 2002). On the other hand, Young and Millar (1999) observed that skuas do not forage at sea when the penguin colonies are sufficient to meet their food requirements. In our study, skuas were frequently observed feeding at Cierva Cove, and no breeding pairs of BS specialized in monopolising parts of the penguin rookery could be identified, as reported for huge penguin rookeries from other Antarctic locations (e.g., Trivelpiece et al. 1980; Young 1994; Hahn and Peter 2003).

Reinhardt et al. (2000) pointed out that the present intensive use of fish by SPS could be related to an increase in the abundance of krill and its predators, fish included (e.g., *E. antarctica* and *P. antarcticum*; Hemmings 1984). This fact, together with the presence of small colonies of penguins at Cierva Point, may account for the important contribution of fish to the diet of both skua species. Alternatively, Votier et al. (2007) pointed out that in larger skua colonies like these, there would be a density-dependent effect, with more fish consumption, apparently due to an increasing interference competition with conspecifics for highly caloric bird meat. This fact may also explain the contribution of fish in the diet of the studied skuas.

On the other hand, the presence of adult penguin feathers in regurgitated pellets is not a direct indicator of predation. These feathers may have rather resulted from scavenging on penguins that had died by other causes, such as predatory attacks from leopard seals *Hydrurga leptonyx* or giant petrels *Macronectes* spp. (Young 1990; Mund and Miller 1995; Schulz and Gales 2004). Besides, Baker and Barbraud (2001) documented that skuas usually fed on faeces of the leopard seal, which are also sources of penguin remains (Green 1986). In fact, field observations at Cierva Point indicated that skuas attacked only penguin chicks and eggs.

In regard to birds other than penguins, skuas themselves emerged as a relatively important food item for the two studied species. This fact contributed to homogenisation of the diet between both species, at least for the reproductive season 1995–96. Cannibalism of adults on eggs and chicks seems to be a frequent behaviour at Cierva Point on the basis of direct observations and prey remains recorded in the field. In a survey conducted in the same locality (Quintana, RD, unpublished data), the mortality rate of SPS offspring due to cannibalism was 77.6%. Likewise, evidence of cannibalism on injured or dead skua adults has also been observed in the study area. From an evolutionary point of view, a high-intraspecific predation risk favours fast chick growth and strong selection pressure promotes the production of high-quality chicks (Ritz 2007).

The frequency of Wilson's storm petrel (*Oceanites oceanicus*) in skua pellets was very low in our study. Nevertheless, the frequent occurrence of remains of this petrel in the field (bones and feathers) suggests that their contribution to skua's diet was underestimated in our results. Indeed, Wilson's storm petrels are very abundant at

Cierva Point, with an estimated population size of 6,500– 7,000 pairs (Quintana et al. 2000). According to Mougeot et al. (1998), the incidence of minor prey species, like this petrel, in skua diets does not reflect local abundance. These authors pointed out that evidence provided by studies involving both pellets and prey remains indicates that these methods underestimate the incidence of small prey, presumably because small birds may often be swallowed whole by skuas.

The low occurrence of the Antarctic tern (*Sterna vittata*) and the absence of the kelp gull (*Larus dominicanus*) in the regurgitated pellets may be explained by their low abundance at Cierva Point (about 4 and 60 breeding pairs in the area, respectively; Quintana et al. 2000), on the basis that skuas feed preferentially on the most abundant and readily obtainable prey species (Norman and Ward 1990; Mougeot et al. 1998).

Fish was a food resource for both skua species, with E. antarctica being the main fish species in their diet. Similarly, at the South Shetlands and Orkney Islands, SPS mainly consumed E. antarctica followed by Gymnoscopelus nicholsi, but Notothenia nudifrons, Gobionotothen gibberifrons and unidentified notothenids were the main fish items of BS (Raya Rey and Montalti 2000). Pleuragramma antarcticum was also present in the diet of both skua species at Cierva Point but to a lesser extent. In contrast, this species was an important item in the diet of SPS in other Antarctic localities (Eklund 1961; Young 1963, 1970, 1994; Le Morvan et al. 1967; Norman and Ward 1990; Mund and Miller 1995; Reinhardt 1997). At Cierva Point, G. nicholsi was not an important food item for SPS, but P. choriodon, which has not been mentioned in previous studies, was relatively common in the diet of BS and SPS. Therefore, differences in the fish species consumed by BS and SPS between Cierva Point and other locations may reflect their abundance at each site.

Raya Rey and Montalti (2000) found refuse in regurgitated pellets of SPS deriving from Antarctic scientific stations, but made no reference to its presence in those of BS. In our study, refuse occurred in regurgitated pellets of both skua species during both breeding seasons. In 1992– 93, refuse was found in a higher proportion in SPS pellets but in a lower proportion in 1995–96. The most likely explanation for this finding is that during the first study period, organic garbage was available at the Argentinean scientific station "Primavera" because it was stored in uncovered containers prior to open burning; to improve waste management in the station, a refuse shed was built thereafter, and skuas had access to garbage by accidental spills only.

The trophic niche of BS was significantly broader than that of SPS, suggesting a more generalist diet. Conversely, some authors (Young 1978; Furness 1987; Ryan and Moloney 1991; Moncorsps et al. 1998; Mougeot et al. 1998) have reported that BS exhibits a very selective diet, especially in Antarctic localities (Mougeot et al. 1998), where they rely mainly on penguin colonies (Trivelpiece et al. 1980; Pietz 1987; Peter et al. 1990; Hahn and Peter 2003). This selectivity for a particular food item could be linked to its high abundance and the maximization of the benefit-to-cost ratio (Moncorsps et al. 1998), as well as to local availability of resources (Moors 1980; Osborne 1985; Zipan and Norman 1993). BS at Cierva Point may have been forced to feed on fish and other seabirds thus broadening their trophic niche because, as stated above, penguins could not fulfil their food requirements.

The present study, conducted at Cierva Point, revealed that during the two studied breeding seasons, SPS consumed more fish and BS more birds, although there was a relative overlap in their diets. Such overlap might possibly be due to, firstly, the important number of skua breeding pairs in the locality, and, secondly, the small penguin colonies, which could not support the food requirements of local skuas, thereby forcing them to supplement their diet by preying on pelagic fish. Further studies on prey availability, foraging strategies and competitive relationships will provide a better understanding of the trophic relationship between both skua species at Cierva Point.

Acknowledgments We want to express our gratitude to the logistic team of the Primavera Station for their cooperation during 1992–93 and 1995–96, to J. L. Agraz, A. Ripalta, O. Benítez, and V. Cirelli for field support, to G. Denari (MACN) and A.Volpedo (FCEyN, UBA) for their help in the analysis of otoliths, and to D. Echeverría, V. Villar, P.Saccone, and G. Rosa for laboratory support. A special thank to Silvia Pietrokovsky for the English translation and to the anonymous reviewers for constructive criticism. This work was supported by the Instituto Antártico Argentino and the University of Buenos Aires.

References

- Agraz JL, Quintana RD, Acero JM (1994) Ecología de los ambientes terrestres de Punta Cierva, Costa de Danco, Península Antártica. Contr Inst Ant Arg 439:1–32
- Baker SC, Barbraud C (2001) Foods of the south polar skua Catharacta maccormicki at Ardery Island, Windmill Islands, Antarctica. Polar Biol 24:59–61
- Barrett RT, Camphuysen KCJ, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64:1675–1691
- Bó MS, Copello S (2001) Distribution and abundance of breeding birds at Deception Island, South Shetland Islands, Antarctica. Mar Ornithol 29:39–42
- Carss DN, Bevan RM, Bonetti A, Cherubini G, Davies J, Doherty D, El Hili A, Feltham MJ, Grade N, Granadeiro JP, Gremillet D, Gromadzka J, Harari Y, Holden T, Keller T, Lariccia G, Mantovani R, McCarthy TM, Mellin M, Menke T, Mirowska-Ibron I, Muller W, Musil P, Nazirides T, Suter W, Trauttmansdorff JFG, Volponi S, Wilson B (1997) Techniques for

assessing cormorant diet and food intake: towards a consensus review. Supplemento alle Ricerche di Biologia della Selvaggina 26:197–230

- Casaux RJ, Barrera-Oro ER (1993) The diet of the blue-eyed shag, *Phalacrocorax atriceps bransfieldensis* feeding in the Bransfield Strait. Antarct Sci 5:335–338
- Coria N, Blendiger PG, Montalti D (1996) The breeding birds of Cape Geddes, Laurie Island, South Orkney Islands, Antarctica. Mar Ornithol 24:43–44
- De Villa-Meza A, Martínez Meyer E, López González C (2002) Ocelot (*Leopardus pardales*) food habits in a tropical deciduous forest of Jalisco, México. Am Midl Nat 148:146–154
- Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. Colon Waterbirds 9:1–17
- Emslie SD, Karnovsky N, Trivelpiece W (1995) Avian predation at penguin colonies on King George Island, Antarctica. Wilson Bull 107:317–327
- Eklund CR (1961) Distribution and life history studies of the south polar skua. Bird Banding 32:187–123
- Favero M, Bellagamba PJ, Farenga M (1991) Abundancia y distribución espacial de las poblaciones de aves de Punta Armonía y Punta Dedo, Isla Nelson, Shetland del Sur. Riv Ital Ornitol 61:85–96
- Favero M, Silva RM, Mauco L (2000) Diet of royal (*Thalasseus masimus*) and sandwich (*T. sandvicensis*) terns during the austral winter in the Buenos Aires Province, Argentina. Ornitol Neotrop 11:259–262
- Furness RW (1987) The skuas. Poyser, Calton
- Furness RW, Hislop JRG (1981) Diets and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. J Zool 195:1–23
- Gales RP (1985) Validation of the stomach-flushing technique for obtaining stomach contents of penguins. Ibis 129:335–343
- Green K (1986) Observations on the food of the south polar skua Catharacta maccormicki near Davis, Antarctica. Polar Biol 6:185–186
- Hahn S, Peter HU (2003) Feeding territoriality and the reproductive consequences in brown skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552–559
- Hemmings AD (1984) Aspects of the breeding biology of McCormicks skua Catharacta maccormicki at Signy Island, South Orkney Islands. Br Antarct Surv Bull 65:65–79
- Hetch T (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J Antarct Res 17:1–87
- Hull C, Carter C, Whitehead MD (1994) Aspects of breeding chronology and success of the Antarctic skua *Catharacta maccormicki* at Magnetic Island, Prydz Bay, Antarctica. Corella 18:37–40
- Hurlbert S (1978) The measurement of niche overlap and some relatives. Ecology 59:67–77
- Jaksic F, Medel R (1987) El acuchillamiento de datos como método de obtención de intervalos de confianza y de prueba de hipótesis para índices ecológicos. Medio Ambiente 8:95–103
- Jackson S, Ryan PG (1986) Differential digestion rates of prey by white-chinned petrels *Procellaria aequinoctialis*. Auk 103:617– 619
- Jackson S, Duffy DC, Jenkins G (1987) Gastric digestion in marine vertebrate predators: in vitro standards. Funct Ecol 1:287–291
- Jahncke J, Rivas C (1998) Recovery, erosion and retention of otoliths in pellets of guanay cormorant: are pellets really good diet indicators? Bol Inst Mar Perú 17:35–46
- Krebs C (1999) Ecological methodology, 2nd edn. Benjamin Cummings, Menlo Park
- Kubetzki U, Garthe S (2003) Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Mar Biol 143:199–207

- Le Morvan P, Mougin JL, Prévost J (1967) Ecologie du skua antarctique (*Stercorarius skua maccormicki*) dans Íarchipel de Pointe Geologie (Terre Adelie). Oiseau 37:193–220
- Maxon SJ, Bernstein NP (1982) Kleptoparasitism by south polar skuas on blue-eyed shags in Antarctica. Wilson Bull 92:157
- Moncorsps S, Chapuis JL, Hanbreux D, Bretagnolle V (1998) Diet of brown skua *Catharacta skua lonnbergi* on the Kerguelen archipelago: comparison between techniques and between islands. Polar Biol 19:9–16
- Montalti D, Soave GE (2002) The birds of Seymour Island, Antarctica. Ornitol Neotrop 13:267–271
- Moors PJ (1980) Southern great skuas on Antipodes Islands, New Zealand: observations on foods, breeding, and growth of chicks. Notornis 27:133–146
- Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen. J Zool 244:429–438
- Müller-Schwarze D, Müller-Schwarze C (1973) Differential predation by south polar skuas in an Adélie penguin rookery. Condor 75:127–131
- Müller-Schwarze D, Müller-Schwarze C (1977) Interaction between south polar skuas and Adélie penguins. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, pp 619–646
- Mund MJ, Miller GD (1995) Diet of the south polar skua *Catharacta* maccormicki at Cape Bird, Ross Island, Antarctica. Polar Biol 15:453–455
- Norman FI, Ward SJ (1990) Foods of the south polar skua at Hop Island, Rauer Group, East Antarctica. Polar Biol 10:489–493
- Norman FI, McFarlane RA, Ward SJ (1994) Carcasses of Adélie penguins as food source for south polar skuas: some preliminary observations. Wilson Bull 106:26–34
- Osborne BC (1985) Aspects of the breeding biology and feeding behaviour of the subantarctic skuas *Catharacta lonnbergi* on Bird Island, South Georgia. Br Antarct Surv Bull 66:57–71
- Parmelee DF, Bernstein NP, Neilson DR (1978) Impact of unfavourable ice conditions on bird productivity at Palmer Station during the 1977–78 field season. Antarct J US 13:146–147
- Peter HU, Kaiser M, Gebaner A (1990) Ecological and morphological investigations on south polar skua (*Catharacta maccormicki*) and brown skua (*Catharacta skua lonnbergi*) on Fildes Peninsula, King George Island, South Getland Islands. Zool JB Syst 117:201–218
- Pietz PJ (1987) Feeding and nesting ecology of sympatric south polar and brown skuas. Auk 104:617–627
- Quintana RD, Cirelli V, Orgeira JL (2000) Abundance and spatial distribution of birds popularions at Cierva Point, Antarctic Peninsula. Mar Ornithol 28:21–27
- Raya Rey AN, Montalti D (2000) Dieta del skua polar del sur Catharacta maccormicki y del skua pardo C. Antarctica. IX Congreso de Biodiversidad y Zoología de Vertebrados, Buenos Aires. pp 112
- Reid K (1996) A guide to the use of otholits in the study of predators at South Georgia. British Antarctic Survery, Cambridge
- Reinhardt K (1997) Nahrung und fütterung antarktischer Raubmöwen Catharacta antarctica lombergi und C. maccormicki. J Ornithol 138:193–213
- Reinhardt K, Hahn S, Peter H-U, Wemhoff H (2000) A review of the diet of southern hemisphere skua. Mar Ornithol 28:7–19
- Ritz MS (2007) Sex-specific mass loss in chick-rearing south polar skuas *Stercorarius maccormicki*: stress induced or adaptive? Ibis 149:156–165
- Ritz MS, Hahn S, Janicke T, Peter H-U (2006) Hydridisation between south polar skua (*Catharacta maccormicki*) and brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region. Polar Biol 29:153–159

- Ryan PG, Moloney CL (1991) Prey selection and temporal variation in the diet of subantarctic skuas at Inaccessible Island, Tristan da Cunha. Ostrich 62:52–58
- Schulz M, Gales R (2004) Winter diet of the subantarctic skua Catharacta antarctica at Macquarie Island. Mar Ornithol 32:179–181
- Siegel S, Castellán NJ (1988) Nonparametric statistics for the behavioural sciences. Mc Graw-Hill, New York
- Thomas D, Taylor E (1990) Study designs and test for comparing resource use and availability. J Wildl Manage 54:332–330
- Trillmich F (1978) Feeding territories and breeding success of south polar skuas. Auk 95:23–33
- Trivelpiece W, Butler RG, Volkman NJ (1980) Feeding territories of brown skuas (*Catharacta lonnbergi*). Auk 97:669–676
- Votier SC, Bearhop S, Ratcliffe N, Furness RW (2001) Pellets as indicators of diet in great skuas *Catharacta skua*. Bird Study 48:373–376
- Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. Polar Biol 26:20–26
- Votier SC, Furness RW, Bearhop S, Crane JE, Caldow RWG, Catry P, Ensor K, Hamer KC, Hudson AV, Kalmbach E, Klomp NI, Pfeiffer S, Philips RA, Prieto I, Thompson DR (2004a) Changes in fisheries discard rates and seabird communities. Nature 427:727–730
- Votier SC, Bearhop S, Ratcliffe N, Philips RA, Furness RW (2004b) Predation by great skuas at a large seabird colony. J Appl Ecol 41:1117–1128

- Votier SC, Bearhop S, Crane JE, Arcos JM, Furness RW (2007) Seabird predation by great skuas: intra-specific competition for food? J Avian Biol 38:234–246
- Williams R, McEldowney A (1990) A guide to the fish otholits from waters of the Australian Antarctic Territory, Heard and Mcquire Islands. ANARE Res Notes 75:1–173
- Young EC (1963) Feeding habits of the south polar skua *Catharacta* maccomircki. Ibis 105:301–318
- Young EC (1970) The techniques of a skua-penguin study. In: Holdgate MW (ed) Antartic ecology. Academic Press, London, pp 568–584
- Young EC (1978) Behavioural ecology of lonnbergi skuas in relation to environment on the Chatham Islands, New Zealand. NZ J Zool 5:401–416
- Young EC (1990) Diet of the south polar skua *Catharacta maccormichi* determined from regurgitated pellets: limitations of a technique. Polar Rec 26:124–125
- Young EC (1994) Skua and penguin: predator and prey. Cambridge University Press, Cambridge
- Young EC, Millar CD (1999) Skua (*Catharacta* sp.) foraging behaviour at the Cape Crozier Adélie penguin (*Pysoscelis* adeliae) colony, Ross Island, Antarctica, and implications for breeding. Notornis 46:287–297
- Zar J (1996) Biostatistical analysis, 4th edn. Prentice-Hall, New Jersey
- Zipan W, Norman FI (1993) Foods of the south polar skua *Catharacta* maccormichi in the eastern Larseman Hills, Princess Elizabeth Land. Polar Biol 13:255–262