

Trophic interactions between brown and south polar skuas at Deception Island, Antarctica

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Abstract It is broadly accepted that the brown skua (*Stercorarius antarcticus lonnbergi*) competitively excludes the south polar skua (*S. maccormicki*) from penguin colonies when breeding sympatrically, forcing the latter to feed on marine resources. The purpose of this work was to examine the diets and trophic niche breadths of each species where they co-occur and to determine the degree of overlap. To this end, we analyzed 169 pellets of brown skuas, collected in two different areas (20 individuals), and 152 of south polar skuas, collected in three different areas (18 individuals), on Deception Island, South Shetland Islands, Antarctica, during the austral summer 2000. Pellet analysis often underestimates the amount of easily digestible prey, but allows for comparisons of the relative contributions of different items in the diet. South polar skuas at our study locations consumed seven different food items and had a trophic niche breadth of 0.133 compared to brown skuas that fed on 10 different items and had a trophic niche breadth of 0.078. The niche overlap between the species was 82.1%. Penguins were the principal food source of both species, however, brown skuas fed mostly on chicks, while south polar skuas fed on adults (carcasses). The use of different age classes of penguins as a food source offers an alternative to competitive exclusion, allowing the coexistence of these species on Deception Island.

Keywords Diet composition · Niche breadth · Niche overlap · South Shetland Islands · *Stercorarius*

Introduction

Brown skuas (*Stercorarius antarcticus lonnbergi*) and south polar skuas (*S. maccormicki*) are opportunistic feeders that take advantage of a number of terrestrial and marine resources including carrion, fish, krill, and other birds (Young 1963; Maxon and Bernstein 1982; Pietz 1987) including skua chicks (Zipan and Norman 1993; Mund and Miller 1995; Malzof and Quintana 2008). The south polar skua breeds along the coasts of the Antarctic continent and outlying islands, while the brown skua is found on northern Antarctic and Sub-Antarctic islands (Eklund 1961; Ritz et al. 2006). These species breed sympatrically in parts of the Antarctic Peninsula and on the South Shetland Islands (Ritz et al. 2006).

Resource partitioning has been observed in areas where these species co-occur (Pietz 1987). This is frequently explained by the monopolization of terrestrial resources (mostly penguins) by brown skuas, which forces south polar skuas to feed on marine resources (Burton 1968; Trivelpiece and Volkman 1982; Hemmings 1984; Pietz 1987) and is attributed to the competitive exclusion of preferred resources by brown skuas (Parmelee and Pietz 1987) due to their greater size and aggressiveness (Pietz 1987). However, aggressive interactions between these species have never been observed, and both skua species have been observed feeding mainly on penguins (Malzof and Quintana 2008; Bertoldi Carneiro et al. 2009) in some locations where they breed sympatrically.

In the absence of brown skuas, south polar skuas feed primarily on terrestrial resources and only rely on marine

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resources occasionally (Norman and Ward 1990; Zipan and Norman 1993; Norman et al. 1994; Mund and Miller 1995); although some pairs of south polar skuas may monopolize penguin colonies forcing others to feed at sea (Young 1994). On some occasions, south polar skuas have been observed using fish as the main resource despite having availability of penguins (Young 1963; Montalti et al. 2009).

The objective of this work was to examine the diet compositions and trophic niche breadths of the south polar and brown skuas where they co-occur and to determine the degree of overlap in order to better understand resource partitioning in these species.

Materials and methods

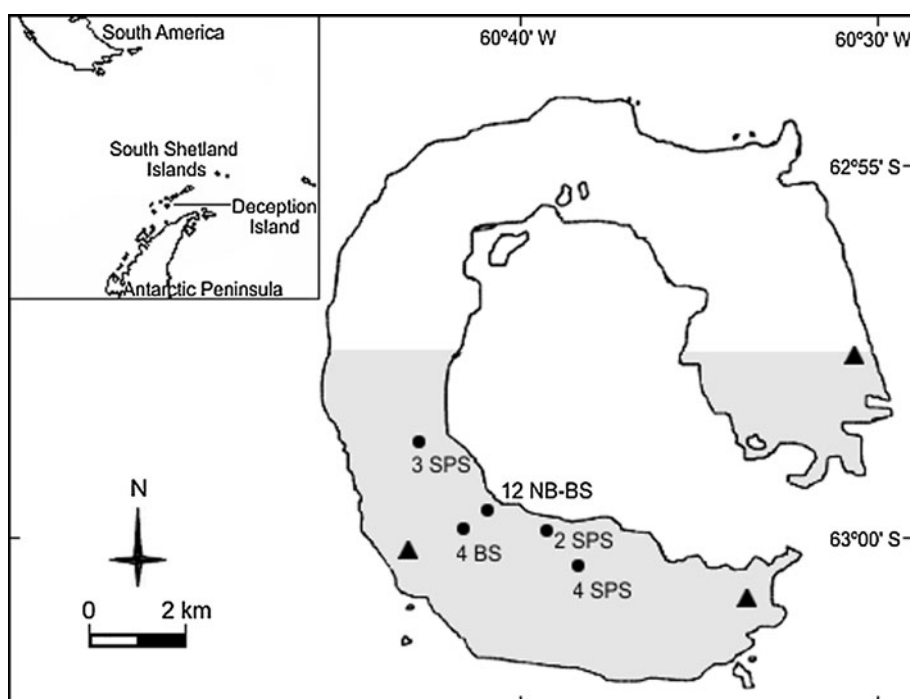
The study was conducted during the breeding season at the southern half of Deception Island, South Shetland Islands, Antarctica ($62^{\circ}57'0''$ S, $60^{\circ}37'60''$ W) (Fig. 1). The study area supports 11 breeding pairs of south polar skuas, 4 breeding pairs of brown skuas, 12 non-breeding brown skuas, and 6,820 pairs of chinstrap penguin (*Pygoscelis antarctica*). In addition, uncensused penguin colonies exist to the south and east of the area (Bó and Copello 2001). A total of 38 skuas and 1,600 chinstrap penguins have also been reported along the internal coast of the island, representing most of the penguins in the area of study (Kendall et al. 2003). The most recent census of the external coast

reported two skua-breeding sites (one of them at our study site) and an estimated 140,000–190,000 chinstrap penguins (Shuford and Spear 1988). In addition to skuas and chinstrap penguins, other birds such as cape petrels (*Daption capense*), Wilson storm petrels (*Oceanites oceanicus*), black-bellied storm petrels (*Fregatta tropica*), Antarctic cormorants (*Phalacrocorax bransfieldensis*), greater sheathbills (*Chionis alba*), kelp gulls (*Larus dominicanus*), and Antarctic terns (*Sterna vittata*) also breed at Deception Island (Olrog 1958; Bó and Copello 2001; Kendall et al. 2003).

We collected a total of 321 pellets from brown ($n = 169$) and south polar skuas ($n = 152$) between January 29 and March 30, 2000. We obtained pellets regurgitated by brown skuas at two locations: one, near Deception Station (Argentinean) where 12 non-breeding skuas congregate (158 pellets) and another, where four breeding pairs congregate (11 pellets). Similarly, we obtained the pellets of south polar skuas at three different areas: one, where three breeding pairs congregate (12 pellets), another with four breeding pairs (26 pellets), and a third near Gabriel de Castilla Station (Spanish), where two pairs are known to breed (four pellets). Pellets were collected irrespective of the individuals that produced them.

We measured the length, width, and height of each pellet and added the three measurements to obtain an index of size and avoid biases due to deformation from storing. The length was measured as the longest line across the pellet, whereas the width and height were represented as

Fig. 1 Study site located on the southern end of Deception Island, South Shetland Islands (gray area). Sites for collection of pellets (filled circle) of south polar (SPS) and brown skuas (BS) pairs and non-breeders (NB), and the numbers in each area are indicated. Locations of penguin colonies (filled triangle) are also shown



two perpendicular lines perpendicular to the length, the longer of which was considered the width. We compared pellet size between the species using a *t* test.

We then classified prey items obtained from the pellets as follows: penguin, flying bird (both recognized by the presence of feathers, bones, and eggshells), fish (recognized by otoliths, crystallines, scales, and vertebral bones), krill, amphipod, mollusk (recognized by the occurrence of shells), and mammal (recognized by bones and hair). We also identified alga, moss, lichen, and stone but did not include these in the analysis, because they do not constitute a nutritional resource. The same pellet could contain more than one kind of item. We further classified penguin remains as adults, chicks, or eggs based on feather characteristics and the level of bone ossification. We considered remains as coming from adult penguins when contour feathers were found and as coming from chicks when only down feathers were found. The latter category may, therefore, include immature (recently fledged) penguins too.

We used otoliths to identify fish remains to the species level and sorted otoliths into right or left to determine the approximate number of fish per pellet. We then used equations in Hecht (1987) to determine the standard length (SL) and mass of all fish prey. A *t* test was performed to compare the mass of the fish used for each skua species when it was allowed by its number.

We determined the ratio of occurrence (RO) of prey items as the proportion of pellets containing each item ($RO = n_i/N$, where n_i is the number of samples in which item *i* was found, and N is the number of samples analyzed). We also calculated the relative ratio of occurrence (RR), which expresses the proportion of prey items by class as a percentage of all prey items in samples ($RR = n_i/\sum n_i$). We performed χ^2 analysis for contingency tables to test the differences in the diets of both skua species, as well as between breeding and non-breeding brown skuas (Zar 1999). Similarly, we calculated RO and RR for prey items from each of penguin subclasses (e.g., adult, chick, and egg) and evaluated differences between species using a χ^2 test and a posteriori test with the Yates' correction for continuity (χ^2_c) to test the differences for each of the categories of penguin (Zar 1999).

We used the Levin index to calculate the trophic niche breadth of brown and south polar skuas from the pellets collected (Colwell and Futuyma 1971). We performed a *t* test to compare the niche breadth index between the species (Zar 1999) and estimated the overlap of the trophic niche using the overlap percentage (Krebs 1989). Finally, we used minimum cut value of 5% (Krebs 1989) to determine the number of frequently used resources.

Results

We identified 205 food items from 169 pellets collected from brown skuas (from two areas with 12 non-breeding and four breeding pairs, respectively) and 208 items from 152 pellets collected from south polar skuas (from three areas with three, two, and four breeding pairs, respectively). Pellet size did not differ significantly between skua species (brown skua: $\bar{x} = 106.62$ mm, $SD = 23.92$ mm, $n = 72$; south polar skua: $\bar{x} = 110.55$ mm, $SD = 25.76$ mm, $n = 48$; $t = -0.86$; $P = 0.3939$).

All seven food classes were represented by items found in brown skua pellets, while mammals were absent from the pellets of south polar skuas. Similarly, we did not find alga or lichen in the pellets of south polar skua. We found stones in 96.5% of the pellets of brown skuas and in 82.2% of those of south polar skuas. We also found remains of refuse (i.e., paper and plastic bags probably from one of the nearby scientific stations) in one brown skua pellet. Those items were not included in the analysis. The size and species of fish consumed by brown and south polar skuas were similar (*Electrona antarctica*: $t = 0.78$; $P = 0.28$) (Table 1).

We found remains of penguins in 94.7% of brown skua pellets and in 88.8% of pellets of south polar skuas. The analyses suggested significant differences between species in their use of penguins ($\chi^2 = 21.05$; $df = 2$; $P < 0.001$), and the post hoc analysis showed differences in their reliance on adult penguins and penguin chicks, but not on penguin eggs (Table 2). We did not find remains of skuas in the pellets of brown skuas in which flying birds were found. Brown skua pellets contained the remains of several flying birds including Wilson storm petrel (one pellet), greater sheathbill (one pellet), southern fulmar (one pellet),

Table 1 Species of fish used by brown and south polar skuas and their estimated standard length (SL) and mass

	Brown skua			South polar skua		
	<i>N</i>	SL (mm)	Mass (g)	<i>N</i>	SL (mm)	Mass (g)
<i>Electrona antarctica</i>	27	65.38 ± 5.84	3.84 ± 1.01	34	64.74 ± 5.02	3.73 ± 0.88
<i>Gymnoscopelus nicholsi</i>	3	171.28 ± 2.98	31.69 ± 1.57	2	173.47 ± 0.52	32.85 ± 0.28
<i>Krefflichthys anderssoni</i>	1	75.95	5.08	–	–	–
<i>G. opisthopterus</i>	–	–	–	1	160.69	43.56

Table 2 Number and frequency of occurrence (in brackets) of the penguin items consumed by brown ($N = 188$) and south polar skuas ($N = 156$) and result of the posteriori comparison with Yates correction for continuity for each penguin item

	Brown skua	South polar skua	χ^2_c	P
Adult	117 (0.622)	126 (0.808)	3.888	0.048
Chick	52 (0.277)	13 (0.083)	15.845	<0.001
Egg	19 (0.101)	17 (0.109)	0.003	0.935

and cape petrels (three pellets). South polar skuas consumed skua chicks (four pellets) as well as Wilson storm petrels (six pellets), snow petrels (four pellets), and cape petrels (six pellets).

RO and RR of prey items showed that both species have a similar pattern in the consumption of penguin as the main food item and some differences in the consumption of the remaining food classes (Table 3). The χ^2 analysis proved the differences in the diets of the two species ($\chi^2 = 23.32$; $df = 6$; $P < 0.001$). Analyses also suggested significant differences in the diets of breeding and non-breeding brown skuas ($\chi^2 = 25.86$; $df = 6$; $P < 0.001$). The trophic niche breadth of the south polar skua, $B_A = 0.191$, was higher than that of the brown skua, $B_A = 0.101$ ($t = -3.61$, $P < 0.001$) with an overlap of 83.9%. The brown skua frequently consumed two resources, penguins and fish, while the south polar skua frequently utilized these as well as flying birds.

Discussion

The collection of pellets allows researchers to obtain a large number of samples with minimum disturbance to birds

Table 3 Number of occurrence (NO), ratio of occurrence (RO), and relative ratio of occurrence (RR) of the different food items found in brown and south polar skuas through analysis of pellets

	Brown skua ($N = 169$)			South polar skua ($N = 152$)		
	NO	RO	RR	NO	RO	RR
Penguin	160	0.947	0.780	135	0.888	0.649
Flying Bird	10	0.059	0.049	35	0.230	0.168
Wilson storm petrel	1	0.006	0.005	6	0.039	0.029
Cape petrel	3	0.018	0.015	6	0.039	0.029
Snow petrel	0	0	0	4	0.026	0.019
Skua chick	0	0	0	4	0.026	0.019
Southern fulmar	1	0.006	0.005	0	0	0
Greater sheathbill	1	0.006	0.005	0	0	0
Unidentified	4	0.024	0.019	15	0.099	0.072
Fish	19	0.112	0.093	25	0.164	0.120
Krill	4	0.024	0.019	5	0.033	0.024
Amphipod	2	0.012	0.010	2	0.013	0.010
Mollusc	4	0.024	0.019	6	0.039	0.029
Mammal	6	0.036	0.029	0	0	0

(Votier et al. 2003; Barrett et al. 2007). Pellet analysis is commonly used to determine the diet composition of sea-birds; however, this method may be biased because it overestimates prey items that are swallowed whole or composed of hard parts and underestimates items ingested in parts or composed of soft tissue (Duffy and Jackson 1986; Votier et al. 2001, Votier et al. 2003). The technique does not allow for the accurate determination of biomass consumed and the subsequent energy gained from it. Thus, this work is not a complete description of the diet of brown and south polar skuas as the method does not allow us to know the nature and proportion of completely digested items.

Despite its disadvantages, pellet analysis is a useful method for diet characterization of seabirds and provides information on the relative importance of different kinds of prey when the same technique is used to compare between different sites and times (Votier et al. 2001; Barrett et al. 2007; Malzof and Quintana 2008). Although the different degree of digestibility of items prevents us from comparing the absolute contribution of each, it allows us to compare their relative contribution to the diets between species. Brown and south polar skuas are closely related phylogenetically. As such, we can expect the same level of digestion for each item and neither underestimation nor overestimation of any item between the species. The close values of RO and RR found in this study may indicate a strong relationship between ingestion of food and production of pellets, similar to that observed in great skuas (*S. skua*) (Votier et al. 2003), and because both species produce pellets after every meal, they provide a useful source of information for investigations into the diets of these species (Votier et al. 2003).

In the present study, pellets were collected from a small number of individuals, and our results may be influenced

by the effects of individual selection and other circumstances that control access to resources. In addition, we show that the diets of breeding and non-breeding brown skuas are different, despite differences in the number of samples. Most of the brown skua pellets used in our analyses were produced by non-breeders, while those of south polar skuas came from breeding individuals. This may be a source of error in our comparison between species, and the difference between species and between breeders and non-breeders might be confounded. The lower energy demand of non-breeders and the lack of pressure to feed offspring frequently are good reasons to expect that mixing samples obtained from breeders and non-breeders may hide the true relationship between the diets of these species.

Diet analysis showed significant differences between the species ($\chi^2 = 23.32$; $df = 6$; $P < 0.001$). Penguins were the item consumed most by both, but the second most common item was flying birds for south polar skuas and fish for brown skuas. In contrast, at Cierva Point, Antarctic Peninsula, the main item for both skua species was fish (Malzof and Quintana 2008).

Similar to other studies, we found south polar skuas consumed more fish than brown skuas (Trivelpiece and Volkman 1982; Reinhardt et al. 2000), despite the importance of fish to the latter's diet. That both species consumed similar amounts, species and sizes of fish suggests that they were obtained in the same way and area, such that, on Deception Island, both species exhibit similar feeding strategies on marine resources. The fish found at Deception Island make daily vertical migrations, only approaching the surface at night (Collins et al. 2008). This suggests skuas may only have access to fish at twilight, or may obtain fish when they are taken to the surface by diving predators. Therefore, the lower reliance on marine resources compared to penguins at this location could be due to the limited availability of fish during most of the day and not to the selection of penguins because of their proximity and ease of access.

We attributed the remains of contour feathers in pellets to adult penguins (although this category also included immature recently fledged chicks) obtained from scavenging, because skuas do not prey on adults but only on their chicks and eggs (Furness 1987; Young 1994; Malzof and Quintana 2008). Penguins were the main resource for both species, but south polar skuas consumed a higher proportion of adults, and brown skuas fed mostly on chicks. This could indicate that brown skuas are more predatory than south polar skuas, which are mostly scavengers. This suggests a partial division in the use of the same resource that could reduce competition between both species.

The limited number of breeding pairs of brown skuas on Deception Island may have facilitated higher levels of

penguin consumption by south polar skuas than has been observed in other sympatric areas. Similarly, non-breeding brown skuas, which made up many of the individuals at this location, may be less aggressive in their defense of penguin resources. None of the brown skua pairs we studied had nests near penguin colonies, which may have enabled them to monopolize this resource (Hahn and Peter 2003). As such, south polar skuas may have had access to all penguin pairs and not only to a portion left free by the brown skuas.

Despite the differences in the diets of both species, niche overlap was over 80%. However, this may not be indicative of competition between skua species if the resources shared are abundant (Colwell and Futuyma 1971). Thus, we cannot state whether there is competition between the species in our study site, only that they share a high proportion of available resources. Niche overlap at Deception Island was higher than observed at Cierva Point (Malzof and Quintana 2008) most likely due to the abundance of penguins available to both species. At Cierva Point, there were 1,014 pairs of gentoo penguin and 182 pairs of skuas (Quintana et al. 2000), whereas the study area at Deception Island supports at least 6,820 pairs of chinstrap penguin for only 15 skua pairs and 12 non-breeding individuals (Bó and Copello 2001), in addition to the big colony of 100,000–150,000 pairs at Bailey Head (Shuford and Spear 1988), close enough to be used by the skuas there. Interference among individuals at Cierva Point might also have led to a less frequent consumption of penguins by individual skuas at that location than at Deception Island (Votier et al. 2007).

At Cierva Point, trophic niche breadth was wider for brown skuas than for south polar skuas (Malzof and Quintana 2008). This is contrary to our results and may reflect the capacity of brown skuas to take advantage of different resources available in a place as well as the diet variability of these species in relation to ecological variables of each site (Reinhardt et al. 2000).

The number, size, and species of fish consumed by skuas were similar for both species at Deception Island. The use of fish at this location was lower than observed at Cierva Point, where the RR (in the cited article RF) of fish was higher than 0.5 for both species (Malzof and Quintana 2008). The differences in fish consumption between locations may be due to the lower availability of penguins at Cierva Point, which may force skuas there to feed more frequently at sea, while at Deception Island, skuas may be less pressured to do so (Young 1963; Trillmich 1978; Young and Millar 1999).

This work contrasts with others that have shown that when breeding sympatrically, brown skuas exclude south polar skuas from penguin colonies, forcing them to feed at sea (Trivelpiece and Volkman 1982; Hemmings 1984; Pietz 1987). Moreover, when combined with observations from studies at other locations, our results highlight the

variability in the feeding strategies exhibited by skuas, which is often difficult to generalize. We show that exclusion of one species by the other from using a resource is not a rule for the coexistence of these species, but that when the amount of resources is enough, they can also share the same resources by using them differentially.

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