Polar Biol (2012) 35:299–304
DOI 10.1007/s00300-011-1054-6

SHORT NOTE

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

**Maricel Graña Grilli · Diego Montalti**

Received: 22 May 2011 / Revised: 14 June 2011 / Accepted: 15 June 2011 / Published online: 5 July 2011

**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

M. Graña Grilli (✉) · D. Montalti
CONICET—Instituto Antártico Argentino,
Cerrito 1248, C1010AAZ Buenos Aires, Argentina
e-mail: ggmaricel@gmail.com

D. Montalti
Sección Ornitología, Facultad de Ciencias Naturales y Museo,
Universidad Nacional de La Plata, Paseo del Bosque,
B1900FWA La Plata, Argentina

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°57′0″ S, 60°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 (*Fregetta 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 (122 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

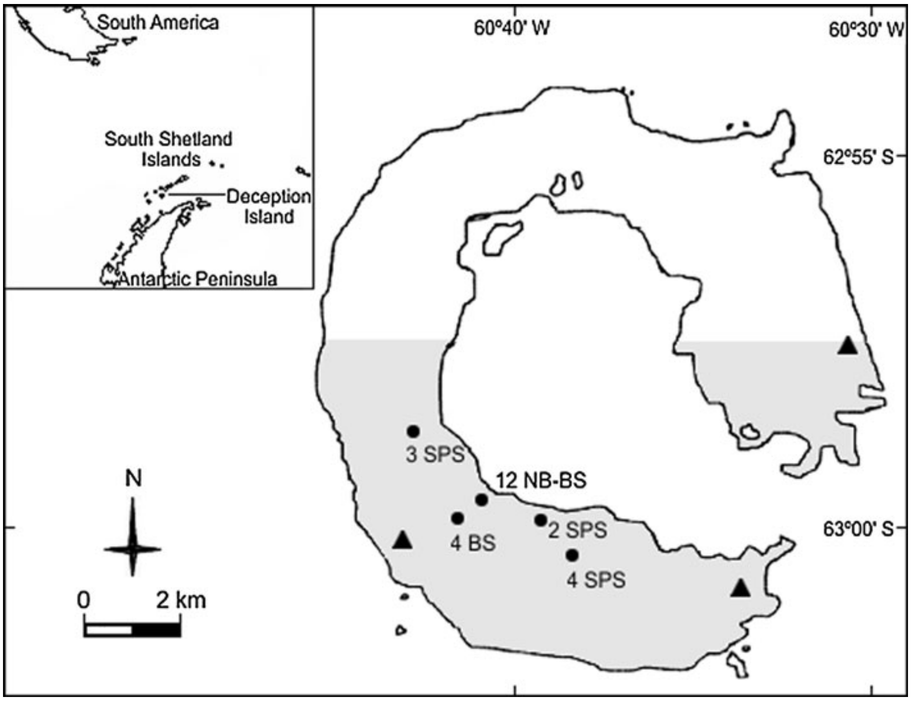

**Fig. 1** Study site located on the southern end of Deception Island, South Shetland Islands (*gray area*). Sites for collection of pellets (*filled circle*) of south polar (*SPS*) and brown skuas (*BS*) pairs and non-breeders (*NB*), and the numbers in each area are indicated. Locations of penguin 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 $\chi^2$ 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 $\chi^2$ test and a posteriori test with the Yates' correction for continuity ($\chi^2_c$) 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 | | |
|---|---|---|---|---|---|---|
| | *N* | SL (mm) | Mass (g) | *N* | SL (mm) | Mass (g) |
| *Electrona antarctica* | 27 | 65.38 ± 5.84 | 3.84 ± 1.01 | 34 | 64.74 ± 5.02 | 3.73 ± 0.88 |
| *Gymnoscopelus nicholsi* | 3 | 171.28 ± 2.98 | 31.69 ± 1.57 | 2 | 173.47 ± 0.52 | 32.85 ± 0.28 |
| *Krefftichthys anderssoni* | 1 | 75.95 | 5.08 | – | – | – |
| *G. opisthopterus* | – | – | – | 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 | $\chi^2_c$ | $P$ |
|---|---|---|---|---|
| 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 $\chi^2$ 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 (Votier et al. 2003; Barrett et al. 2007). Pellet analysis is commonly used to determine the diet composition of seabirds; 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

**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 |

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.

**Acknowledgments** We thank M. S. Bó and S. Copello for their participation in the field work and M. Libertelli for assistance with lab work. The Instituto Antártico Argentino gave permission and financial support. We are also grateful to S. Votier and other reviewers whose observations helped us to improve this manuscript. Finally, we are very grateful to Daniel Brooks and the Editorial Assistance Program of the Association of Field Ornithologists and to Melanie Colon who, through that program, improved the English and made useful comments on the manuscript.

## References

Barrett RT, Camphuysen CJ, 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

Bertoldi Carneiro AP, Polito MJ, Sander M, Trivelpiece WZ (2009) Abundance and spatial distribution of sympatrically breeding *Catharacta* spp. (skuas) in Admiralty Bay, King George Island, Antarctica. Polar Biol 33:673–682. doi:10.1007/s00300-009-0743-x

Bó MS, Copello S (2001) Distribution and abundance of breeding birds at Deception Island, South Shetland Islands, Antarctica, February to April 2000. Mar Ornithol 29:39–42

Burton RW (1968) Breeding biology of the brown skua *Catharacta skua lönnbergi* (Mathews) at Signy Island, South Orkney Islands. Br Antarct Surv Bull 15:9–28

Collins MA, Xavier JC, Johnston NM, North AW, Enderlein P, Tarling GA, Waluda CM, Hawker EJ, Cunningham NJ (2008) Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biol 31:837–851. doi:10.1007/s00300-008-0423-2

Colwell RK, Futuyma DJ (1971) On the measurements of niche breadth and overlap. Ecology 52:567–576

Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. Colonial Waterbirds 9:1–17

Eklund CR (1961) Distribution and life history studies of the south-polar skua. Bird Banding 32:187–223

Furness RW (1987) The skuas. Poyser, Calton

Hahn S, Peter H-U (2003) Feeding territoriality and the reproductive consequences in brown skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552–559. doi:10.1007/s00300-003-0522-z

Hecht T (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J Antarct Res 17:1–87

Hemmings AD (1984) Aspects of the breeding biology of McCormich's skua *Catharacta maccormicki* at Signy Island, South Orkney Islands. Br Antact Sur Bull 65:65–79

Kendall KA, Ruhl HA, Wilson RC (2003) Distribution and abundance of marine bird and pinniped populations within Port Foster, Deception Island, Antarctica. Deep-Sea Res Pt II 50:1873–1888. doi:10.1016/S0967-0645(03)00096-1

Krebs CJ (1989) Ecological methodology. HarperCollins Publishers, New York

Malzof SL, Quintana RD (2008) Diet of the south polar skua *Catharacta maccormicki* and the brown skua *C. antarctica lonnbergi* at Cierva Point, Antarctic Peninsula. Polar Biol 31:827–835. doi:10.1007/s00300-008-0421-4

Maxon SJ, Bernstein NP (1982) Kleptoparasitism by south polar skuas on blue-eyed shags in Antarctica. Wilson Bull 94:269–281

Montalti D, Casaux R, Coria NR, Soave G, Graña Grilli M (2009) The importance of fish in the diet of the south polar skua *Stercorarius maccormicki* at the South Shetland Islands, Antarctica. Emu 109:305–309. doi:10.1071/MU09042

Mund MJ, Miller GD (1995) Diet of the south polar skua *Catharacta maccormicki* at Cape Bird, Ross Island, Antarctica. Polar Biol 15:453–455. doi:10.1007/BF00239723

Norman FI, Ward SJ (1990) Foods of the south polar skua at Hop Island, Rauer Group, East Antarctica. Polar Biol 10:489–493. doi:10.1007/BF00233696

Norman FI, McFarlane RA, Ward SJ (1994) Carcasses of Adelie penguins as a food source for south polar skuas: some preliminary observations. Wilson Bull 106:26–34

Olrog CC (1958) Observaciones sobre la avifauna antártica y de alta mar desde el Río de La Plata hasta los 60° de latitud Sur. Acta Zool Lilloana 15:19–33

Parmelee DF, Pietz PJ (1987) Philopatry, mate and nest-site fidelity in the brown skuas of Anvers Island, Antarctica. Condor 89:916–919

Pietz PJ (1987) Feeding and nesting ecology of sympatric south polar and brown skuas. Auk 104:117–127

Quintana RD, Cirelli V, Orgeira JL (2000) Abundance and spatial distribution of bird populations at Cierva Point, Antarctic Peninsula. Mar Ornithol 28:21–27

Reinhardt K, Hahn S, Peter H-U, Wemhoff H (2000) A review of the diets of southern hemisphere skuas. Mar Ornithol 28:7–19

Ritz MS, Hahn S, Janicke T, Peter H-U (2006) Hybridisation between south polar skua (*Catharacta maccormicki*) and brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region. Polar Biol 29:153–159. doi:10.1007/s00300-005-0034-0

Shuford WD, Spear LB (1988) Surveys of breeding penguins and other seabirds in the South Shetland Islands, Antarctica, January–February 1987. NOAA Technical Memorandum NMFS-F/NEC-59, U.S. Department of Commerce, Massachusetts

Trillmich F (1978) Feeding territories and breeding success of south polar skuas. Auk 95:23–33

Trivelpiece W, Volkman NJ (1982) Feeding strategies of sympatric south polar *Catharacta maccormicki* and brown skuas *C. lönnbergi*. Ibis 152:50–54. doi:10.1111/j.1474-919X.1982.tb03740.x

Votier SC, Bearhop S, Ratcliffe N, Furness RW (2001) Pellets as indicators of diet in great skuas *Catharacta skua*. Bird Study 48:373–376. doi:10.1080/00063650109461237

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. doi:10.1007/s00300-002-0446-z

Votier SC, Bearhop S, Crane JE, Arcos JM, Furness RW (2007) Seabird predation by great skuas *Stercorarius skua*—intra-specific competition for food. J Avian Biol 38:234–246. doi:10.1111/j.2007.0908-8857.03893.x

Young EC (1963) Feeding habits of the south polar skua *Catharacta maccormicki*. Ibis 105:301–318. doi:10.1111/j.1474-919X.1963.tb02509.x

Young E (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 Adelie Penguin *(Pygoscelis adeliae)* colony, Ross Island, Antarctica, and implications for breeding. Notornis 46:287–297

Zar JH (1999) Biostatistical analysis. Prentice-Hall, New Jersey

Zipan W, Norman FI (1993) Foods of the south polar skua *Catharacta maccormicki* in the eastern Larsemann Hills, Princess Elizabeth Land, East Antarctica. Polar Biol 13:255–262. doi:10.1007/BF00238761