# A REVIEW OF THE DIETS OF SOUTHERN HEMISPHERE SKUAS

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**SUMMARY**

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The diets of Southern Hemisphere skuas *Catharacta* sp. are reviewed. Data from 189 sources were analyzed and are separately presented for the breeding and non-breeding season, and for eight different regions: (1) Tierra del Fuego, (2) the Falkland Islands, (3) South Georgia, (4) the Tristan da Cunha and Gough Island group, (5) the Antarctic Peninsula, the South Shetland and South Orkney Islands, (6) the continental coast of Antarctica, (7) the Prince Edward, Crozet, Kerguelen and Heard Island groups, and (8) Macquarie Island, the Chatham, Antipodes and Snares Islands, according to both taxonomy and the main distribution areas. We furthermore present the mode of foraging employed by skuas as well as the method of sampling by the observer. Semi-quantitative investigations have been carried out in only 12 studies. A total of 110 food items has been identified to species level.

## INTRODUCTION

Skuas of the Northern Hemisphere feed on a variety of items and use different foraging techniques (Furness 1987). From the literature it became evident that the same holds true also for their southern counterparts. A detailed knowledge of food composition and consumption appears to be an important research object because reproduction is known to be affected by changes in food abundance in the Great Skua *Catharacta skua* as well as in the Arctic Skua *Stercorarius parasiticus* (Furness & Hislop 1981, Hamer *et al.* 1991, Phillips *et al.* 1996). Food availability also appears to be the most important factor that explains the latitudinal gradient in the breeding success of Southern Hemisphere skuas (Reinhardt 1997a). The aim of the present paper is to provide a review of the published records of food items of Southern Hemisphere skuas *Catharacta* sp. With the presentation of quantitative data we hope to encourage energetic studies by the use of Nagy's (1987) equations for quantitative foodweb modelling. A further aspect is the variety of different predator-prey interactions. Therefore, food categories are presented on the species level if possible. Recent studies found that diet differences are often the result of different sampling techniques (Young 1990, Moncorps *et al*. 1998, Reinhardt 1998). Sampling techniques are, therefore, also presented.

## METHODS

Data on the food of southern Hemisphere skuas were obtained from the literature. The five skua taxa considered, following the classification of Furness (1996), are Chilean Skua *Catharacta chilensis*, Falkland Skua *C. antarctica antarctica*, Tristan Skua *C. antarctica hamiltoni*, Brown Skua *C. antarctica lonnbergi* and South Polar Skua *C. maccormicki.* As a further category, mixed pairs and pairs of hybrids were included. The latter refer to pairs between *C. maccormicki* x *C. a. lonnbergi*.

Food items are given to the species level if possible, whereby no separation was made between the status of these prey (e.g. eggs, chicks, fledglings). Plant material has been excluded from the analysis, although it can be commonly obtained by stomach flushing (K. Reinhardt unpubl. data).

Study sites were pooled for different regions: (1) Tierra del Fuego, (2) the Falkland Islands, (3) South Georgia, (4) the Tristan da Cunha and Gough Island group, (5) the Antarctic Peninsula, the South Shetland and South Orkney Islands, (6) the continental coast of Antarctica, (7) the Prince Edward, Crozet, Kerguelen and Heard Island groups, and (8) Macquarie Island, the Chatham Islands, the Antipodes and the Snares Islands. These groupings are somewhat arbitrary but were summarized mainly for reasons of skua taxonomy, with the Chilean Skua exclusively occurring in region (1) and the Patagonian coast, the Falkland Skua in region (2) and the Patagonian coast, and the Tristan Skua in region (4). The South Polar Skua is to be found in region (6) whereas skuas from regions (3), (7) and (8) belong to the Brown Skua. The latter and the South Polar Skua share region (5) in their distribution range and hybridize there (e.g. Parmelee 1988). A.D. Hemmings (pers. comm.) has suggested a division into climatic regions (temperate, sub-Antarctic, maritime Antarctic and continental Antarctic) which also seems a practical approach. The few quantitative studies (see below) correspond to both, the latter groupings as well as to skua taxonomy (see also Fig. 1).

The foraging strategy of skuas, viz. scavenging (S), predation (P), or kleptoparasitism (K) and the sampling technique of the observer: direct observation (O), ligature method, spontaneous regurgitations (R), stomach contents obtained by flushing or killing birds (C), the collection of prey remains and pellets around the nest or at middens (P), and faecal samples (F), have been recorded.

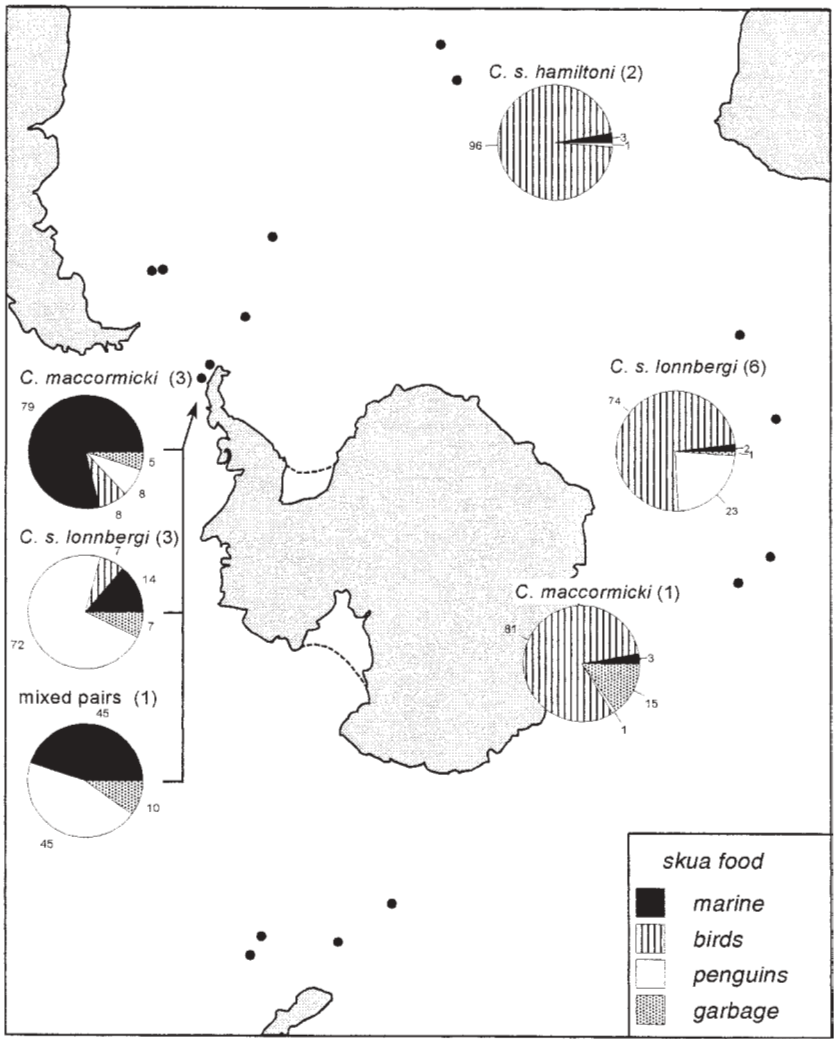


***Fig. 1.*** *Food studies that provide semi-quantitative data (percentage figures) for Southern Hemisphere skuas, with four categories. 'Marine food' includes fish, krill and other crustaceans, cephalopods and other marine invertebrates, 'Birds' includes adult flying birds, their chicks and eggs, and also small mammals, 'Penguins' refers to eggs and chicks and carcasses of penguins, 'Garbage' contains kitchen refuse as well as seal carcasses. Numbers in parentheses are the number of studies, the circles represent average values of food in these studies. The diagrams are based upon Adams (1982), Fraser (1984), Hunter (1990), Peter* et al. *(1990), Pietz (1987), Ryan & Moloney (1991), Stahl & Mougin (1986), Wang & Norman (1994), Moncorps* et al. *(1998) and Mougeot* et al. *(1998). Quantitative studies (e.g. mass percentage composition of the food – Montalti* et al. *(1996) and Reinhardt (1997b) are excluded. Both studies revealed an even higher importance of fish in the diet of the South Polar Skua in region 5 (the Antarctic Peninsula, the South Shetland and South Orkney Islands).*

It was further noted whether the record was from within or outside the breeding season and whether there was sympatric occurrence with one of the different skua taxa. Data from unpublished theses as well as other unpublished observations were included if available. Only original data were considered, general statements as 'skuas take eggs and chicks of all petrel species' are not included here, neither is information such as 'skuas may take chicks' of certain species. Reviews (e.g. Watson 1975) are usually not considered unless they contain until then unpublished information or it is clear that original research is presented. From papers that report on the same information (e.g. Wang 1991, Wang & Norman 1993, Wang *et al.* 1996) the versions with the least information have been excluded. Especially in the older literature it was impossible to decide whether a particular author referred to the South Polar or the Brown Skua, such cases were not considered. Except for the Chilean Skua, incidences of cannibalism are generally very high among skuas (e.g. Young 1963b, Pietz 1987, Peter *et al.* 1990, Wang 1994, Z. Wang pers. comm.). Very often, the evidence of cannibalism is obtained by the observation of dead chicks. Cannibalism is therefore difficult to distinguish from siblicide which serves a different function (e.g. Young 1963a, Spellerberg 1971). It does not necessarily result in the eating of the chick. Cannibalism is, therefore, not dealt with in detail here.

A first draft of the paper was distributed among eight skua biologists on all continents with the request for help and was tabled at the Scientific Committee on Antarctic Research (SCAR) Bird Biology Subcommittee meeting in 1996 in Cambridge, U.K. This resulted in additional information being received from four biologists. Deadline for our review was 1 August 1998.

Sources of data in tables are numbered and refer to the numbered, alphabetical list of references. Common and scientific names follow those of Higgins & Davies (1996).

**TABLE 1**

**Food of skuas during the non-breeding season**

| Taxa | Food | Foraging mode | Region | Reference |
|---|---|---|---|---|
| Brown Skua | Hartlaub's Gull *Larus hartlaubii* | P | SW of Cape of Good Hope | 146 |
| | Silver Gull *L. novaehollandiae* | ? | New Zealand | 158 |
| | White-fronted Tern *Sterna striata* | P | Islands south off New Zealand | 54 |
| | Broad-billed Prion *Pachyptila vittata* | P | Islands south off New Zealand | 60 |
| | petrels, unidentified | ? | Balleny Island | 137 |
| | diving petrels, unidentified | ? | Solander Island | 25 |
| | penguins, unidentified | ? | Balleny Island | 137 |
| | barnacle *Lepas australis* | P | Islands south off New Zealand | 60 |
| | abalone *Haliotis virginea* | P | Islands south off New Zealand | 60 |
| | garbage, cephalopods | S | Australian coast | 156 |
| | sheep flesh | S | Islands south off New Zealand | 22 |
| | sheep flesh | S | Maritime Antarctic | 111 |
| | fisheries refuse | S | Tasman Sea, Australian Shelf, SW of Cape of Good Hope | 10, 25, 82, 146 |
| South Polar Skua | sheep flesh | S | Maritime Antarctic | 111 |

**TABLE 2**

**Food of the Chilean Skua**

| Food item | Foraging mode | Sampling technique | Reference |
|---|---|---|---|
| penguins, unidentified | S | C | 63 |
| diving petrels *Pelecanoides* sp. | ? | P | 129 |
| goose *Chloeophaga* sp. | ? | P | 129 |
| Nutria *Myocastor coypus* | ? | P | 129 |
| fish, unidentified | K, S | O, C, R | 12, 62, 63, 129, 133 |
| crustaceans ('red shrimp') | ? | C | 132 |
| cirripeds ? | C | 63 | |
| garbage meat | S | C | 63 |
| 'fish etc.' (?) | ? | C | 141 |

**TABLE 3**

**Food of the Falkland Skua**

| Food item | Foraging mode | Sampling technique | Reference |
|---|---|---|---|
| **Penguins** | | | |
| King Penguin *Aptenodytes patagonicus* | P, S | O | 127 |
| Gentoo Penguin *Pygoscelis papua* | P | O | 30, 75, 76, 127, 153, 157 |
| Rockhopper Penguin *Eudyptes chrysocome* | P, S | O | 30, 76, 127, 157 |
| penguins, unidentified | P, S | ? | 182 |
| **Flying birds** | | | |
| Black-browed Albatross *Thalassarche melanophrys* | ? | ? | 76 |
| Slender-billed Prion *Pachyptila belcheri* | P | P | 30, 76, 157 |
| Magellan Goose *Chloeophaga picta* | P, S | ? | 181,182 |
| Falkl. Is. Flightless Steamer Duck *Tachyeres brachypterus* | P | ? | 181 |
| Imperial Cormorant *Phalacrocorax atriceps* | ? | ? | 30, 76 |
| cormorant *Phalacrocorax* sp. | P | ? | 110, 181 |
| **Mammals** | | | |
| sheep *Ovis aries* | S | O | 182 |

## RESULTS

### Qualitative data

*Non-breeding season*

There is very little information on the food of skuas in the non-breeding season. The most important is that by Hemmings (1990b) which refers to Brown Skuas being winter residents at the Chatham Islands (Table 1). Veit (1978) noted that South Polar Skuas at 40°N, 67°W were in the vicinity of fishing trawlers, altough no information was given whether the skuas scavenged on the fisheries refuse or were kleptoparasitic on other birds. Moncorps *et al.* (1998) found diet differences between breeding and non-breeding individuals within the breeding season.

*Breeding season*

Chilean Skua *C. chilensis*

There are very few references on the food of this species (Table 2). The only information we have is from Tierra del Fuego. Its feeding habits from other breeding areas are unknown.

Falkland Skua *C. antarctica antarctica*

The literature research revealed a surprisingly poor knowledge of the food of the Falkland Skua (Table 3). There is clearly a lack of published data although quantitative data for the predation of skuas on prions *Pachyptila* sp. exist (I. Strange pers. comm.). The exceptional poor situation becomes obvious with the fact that up to now apparently no published data about skua predation on King Penguins *Aptenodytes patagonicus* exists.

Tristan Skua *C. antarctica hamiltoni*

The food of the Tristan Skua seems to be fairly constant, most prey items have been recorded by more than one observer (Table 4). The food consists mainly of penguins, burrowing seabirds and small mammals. It usually includes a small proportion of landbirds. Food samples have mostly been obtained by collecting regurgitated pellets.

Brown Skua *C. antarctica lonnbergi*

The diet of the Brown Skua is shown in Table 5. Collecting pellets or prey remains and direct observation have been the main sources of information. Although the diets are recorded from regions that are quite far apart, one-fourth of the food items are shared between at least two regions. As can be seen from Table 5, the Brown Skua generally feeds on eggs and chicks of penguins, burrowing petrels and seal carcasses or placentae, irrespective of whether it breeds on South Georgia, or on the islands in the southern Pacific and southern Indian Oceans.

**TABLE 4**

**Food of the Tristan Skua**

| Food species | Foraging mode | Sampling technique | Reference |
|---|---|---|---|
| **Penguins** | | | |
| Rockhopper Penguin *Eudyptes chrysocome* | S | O, P | 41, 42, 50, 138, 139, 144 |
| **Flying birds** | | | |
| Antarctic Prion *Pachyptila desolata* | ? | P | 41, 138 |
| Broad-billed Prion *P. vittata* | P | P | 41, 42, 139, 144, 179 |
| Grey Petrel *Procellaria cinerea* | P | P | 42 |
| ? White-chinned Petrel *P. aequinoctialis* | ? | P | 50 |
| Great Shearwater *Puffinus gravis* | P | P | 41, 42, 50, 138, 139 |
| Little Shearwater *P. assimilis* | P | P | 41, 42, 138, 139 |
| Atlantic Petrel *Pterodroma incerta* | P | P | 33 |
| Great-winged Petrel *P. macroptera* | ? | P | 139 |
| Kerguelen Petrel *P. brevirostris* | P | P | 41, 42 |
| Soft-plumaged Petrel *P. mollis* | ? | P | 41, 42, 139, 144, 179 |
| White-bellied Storm Petrel *Fregetta grallaria* | ? | P | 41, 138, 139 |
| White-faced Storm Petrel *Pelagodroma marina* | ? | P | 41, 42, 138, 139 |
| Common Diving Petrel *Pelecanoides urinatrix* | ? | P | 41, 42, 138, 139 |
| Inaccessible Island Rail *Atlantisia rogersi* | ? | P | 41, 50, 138, 139 |
| Tristan Moorhen *Gallinula comeri* | P | R | 36 |
| Tristan Trush *Nesocichla eremita* | ? | P | 41, 138, 139 |
| Nightingale Finch *Neospiza acunhae* | ? | P | 41, 139 |
| **Mammals** | | | |
| rats *Rattus* sp. | ? | P | 139 |
| House Mouse *Mus musculus* | ? | P | 144 |
| **Invertebrates** | | | |
| barnacles *Lepas* sp. | ? | P | 41, 50, 139 |

**TABLE 5**

**Food of the Brown Skua in different regions during the breeding season obtained by different sampling methods. For the location of the regions see Methods section**

| Food species | Sampling method per region | | | Reference |
|---|---|---|---|---|
| | 3 | 7 | 8 | |
| **Penguins** | | | | |
| King Penguin *Aptenodytes patagonicus* | P, O | P, O | | 9, 66, 127, 142, 152, 165 |
| Gentoo Penguin *Pygoscelis papua* | P, O | P | P | 101, 107, 127, 142, 145, 152, 155 |
| Macaroni Penguin *Eudyptes chrysolophus* | P | O, ? | | 9, 16, 31, 101, 146, 152 |
| Rockhopper Penguin *E. chrysocome* | | P, O | P | 2, 84, 142, 145, 146, 152, 153 |
| Royal Penguin *E. schlegeli* | | | P | 72, 145 |
| Little Penguin *Eudyptula minor* | | | ? | 39 |
| penguins, unidentified | | O | O | 9, 27, 152, 173 |
| **Flying birds** | | | | |
| Black-browed Albatross *Thalassarche melanophrys* | P | | | 101 |
| Grey-headed Albatross *T. chrysostoma* | P | O | | 101, 146 |
| Chatham Albatross *T. eremita* | | | O | 39 |
| Wandering Albatross *Diomedea exulans* | O | | | 53 |
| sooty albatross *Phoebetria* sp. | | P | | 79, 142, 152 |
| Southern Giant Petrel *Macronectes giganteus* | O | P | | 53, 101, 152 |
| Northern Giant Petrel *M. halli* | P | | | 101 |
| Blue Petrel *Halobaena caerulea* | | P | P | 2, 46, 65, 71, 86, 88, 102, 107, 131, 142, 148, 152, 159 |
| Antarctic Prion *Pachyptila desolata* | P | P | P | 14, 67, 71, 79, 83, 86, 88, 101, 145, 148, 152, 160, 165 |
| Broad-billed Prion *P. vittata* | | P, O | P, O | 2, 13, 58, 65, 83, 142, 146, 152, 159, 186, 189 |
| Salvin's Prion *P. salvini* | | P | P | 1, 131, 159 |
| Thin-billed Prion *P. belcheri* | | P | | 88 |
| Fairy Prion *P. turtur* | | | P | 83, 84, 148, 173 |
| prions, unidentified | | P | P | 46, 154 |
| Grey Petrel *Procellaria cinerea* | | P | P | 71, 84, 88 |
| White-chinned Petrel *P. aequinoctialis* | P | P | P | 1, 2, 46, 79, 84, 101, 131, 142, 152 |
| Little Shearwater *Puffinus assimilis* | | | P | 83, 84 |
| Short-tailed Shearwater *P. tenuirostris* | | | P | 84 |
| Sooty Shearwater *P. griseus* | | | P | 71, 84, 145, 148, 154, 159 |
| Great-winged Petrel *Pterodroma macroptera* | | P | | 1, 2, 46, 86, 88, 107, 131, 142, 152 |
| Kerguelen Petrel *P. brevirostris* | | P, O | | 1, 2, 86, 131, 142, 146, 152 |
| Mottled Petrel *P. inexpectata* | | | P | 83, 157 |
| Soft-plumaged Petrel *P. mollis* | | P, O | P | 1, 2, 46, 71, 84, 131, 142, 148, 152 |
| White-headed Petrel *P. lessoni* | | P | P | 71, 84, 86, 88, 107, 145, 148, 152, 154, 159 |
| petrels *Pterodroma* sp. | | | P | 134 |
| Black-bellied Storm Petrel *Fregetta tropica* | P | P | P | 84, 101, 131, 152 |
| Grey-backed Storm Petrel *Garrodia nereis* | | P | P | 84, 88, 152, 173 |
| White-faced Storm Petrel *Pelagodroma marina* | | P | P, O | 134, 154, 186, 189 |
| Wilson's Storm Petrel *Oceanites oceanicus* | P | P | | 101, 152 |
| Common Diving Petrel *Pelecanoides urinatrix* | P, O | P | P | 58, 71, 83, 84, 88, 101, 108, 134, 148, 152, 159, 173, 186 |
| South Georgia Diving Petrel *P. georgicus* | P, O | P, O | | 86, 107, 108, 142, 152 |
| diving petrels, unidentified | | O | | 146 |
| Imperial Cormorant *Phalacrocorax atriceps* | | P | | 86, 131 |
| Brown Teal *Anas aucklandica aucklandica/nesiotis* | | | P | 159 |
| Northern Pintail *A. acuta eatoni* | | O, P | | 9, 86, 123 |
| Pacific Black Duck *A. superciliosa* | | | P | 145 |
| Yellow-billed Pintail *A. georgica* | O, P | | | 93, 101 |
| Kelp Gull *Larus dominicanus* | O | P | O | 46, 110, 134, 186 |
| Antarctic Tern *Sterna vittata* | O | | P | 84, 110 |
| Kerguelen Tern *S. virgata* | | P, O | | 86, 107 |
| Lessser Sheathbill *Chionis minor* | | P | | 1, 131, 142, 152 |
| Greater Sheathbill *C. alba* | | P | | 46, 88 |
| Kaka *Nestor meridionalis* | | | P | 134 |
| South Georgia Pipit *Anthus antarcticus* | P | | | 135 |

**(TABLE 5 continued)**

| Food species | Sampling method per region | | | Reference |
|---|---|---|---|---|
| | 3 | 7 | 8 | |
| **Mammals** | | | | |
| Southern Elephant Seal *Mirounga leonina* | P, O | P, O | P, O | 7, 9, 67, 69, 72, 107, 120, 142, 145, 146, 148, 152, 155 |
| Antarctic Fur Seal *Arctocephalus gazella* | P, O | | | 127, 152, 155 |
| Hooker's Sea Lion *Otaria hookeri* | | O | | 18 |
| rats *Rattus* sp. | P | O, C | P | 9, 145, 152, 155 |
| House Mouse *Mus musculus* | | P | | 88, 178 |
| Rabbit *Oryctolagus cuniculus* | | P | P | 18, 29, 67, 72, 86, 145, 148, 152 |
| Sheep *Ovis aries* | | | O | 186 |
| **Fish** | | | | |
| *Notothenia* sp. | | P | | 152 |
| unidentified | | O, C | | 107 |
| **Invertebrates** | | | | |
| mussels, unidentified | O | | | 177 |
| chiton *Plaxiphora aurea* | | | P | 145 |
| *Nacella deaurata* | | P | | 152 |
| *Cantharidus coruscans* | | | P | 145 |
| *Cyanoramphus* sp. | | | P | 84 |
| goose barnacle *Lepas anatifera* | | P | P | 145, 152 |
| krill *Euphausia* sp. | O | | | 155 |
| copepods, unidentified | O | | | 152 |
| amphipods, unidentified | O | | | 155 |
| cephalopods, unidentified | | P | | 155 |
| **Other items** | | | | |
| kitchen refuse | O | P, O | | 146, 152, 155, 165 |
| fisheries refuse | | O | | 146 |

Diet records from the region of sympatric breeding with the South Polar Skua are given in Table 7.

South Polar Skua *C. maccormicki*

The South Polar Skua usually exploits large terrestrial colonies of seabirds, and also feeds extensively on fish (Table 6). Seal carcasses and garbage are also used. Marine invertebrates including krill *Euphausia* spp. are used to a lesser extent, but distinctly more frequently than by the different skua forms. For the species' diet in the region of the Antarctic Peninsula, the South Shetlands and South Orkneys where it breeds sympatrically with the Brown Skua and mixed pairs see Table 7.

Hybrid skuas

The data available for mixed pairs from Brown and the South Polar Skuas are summarized in Table 7. For reasons of comparison, the known diets of Brown and South Polar Skuas in their sympatric breeding range are included.

In a hybrid pair between a South Polar Skua and a Chilean Skua hybrid (Reinhardt *et al.* 1997), the myctophid fish *Electrona antarctica* was recorded in the diet (K. Reinhardt unpubl. data).

Southern Hemisphere skuas also employ kleptoparasitism as a feeding habit (e.g. Milledge 1977, Wahl 1977, reviewed in Higgins & Davis 1996). It appears that this technique is used more frequently during the non-breeding season at sea (Sinclair 1980, Watson 1975, Spear & Ainley 1993). Hereby, only fish, marine invertebrates and floating carrion can be obtained, being the main source during this time anyway. In some cases, skuas snatch food from seals or humans. This behaviour is difficult to distinguish from scavenging. There is slight evidence from personal observations and Behn *et al.* (1955) that the Chilean Skua employs kleptoparasitism to a larger extent than do the other skuas.

**Quantitative data**

Green (1986), Mund & Miller (1995), Norman & Ward (1990), Wang (1992), and Young (1990) use the incidence (the percentage of occurrence of each food item in the collected samples) as a semi-quantitative measure. From that, a quantification of the relative abundance (as, in part, done by Mougeot *et al.* 1998) and the total food consumption is impossible. Adams (1982), Fraser (1984), Hunter (1990), Peter *et al.* (1990), Pietz (1987), Ryan & Moloney (1991), Stahl & Mougin (1986), Wang & Norman (1994), Mougeot *et al.* (1998) and Moncorps *et al.* (1998) give the percentage distribution of the food items in a sample that is assumed to be representative for the total diet. Figure 1 shows the results of these studies in a geographical distribution. In those studies data from direct observations, from collecting pellets or prey remains, as well as from spontaneous regurgitations are usually combined. Calculations from pellet components underestimate the soft items such as station garbage, fish and carrion flesh (Young 1990). They are, therefore, hardly comparable to different techniques. A few studies attempted to calculate the total consumption by a skua population. Haftorn *et al.* (1991b) counted daily the number of chicks of the Antarctic Petrel *Thalassoica antarctica* that were found

**TABLE 6**

**Food of the South Polar Skua in continental Antarctica obtained by different sampling methods**

| Food item | Foraging mode | Sampling technique | Reference |
|---|---|---|---|
| **Penguins** | | | |
| Emperor Penguin *Aptenodytes forsteri* | S | P | 87, 119, 171, 180 |
| Adélie Penguin *Pygoscelis adeliae* | S, P | P, O, R, F | 4, 21, 26, 34, 45, 78, 90, 91, 92, 97, 98, 106, 109, 119, 161, 171, 180, 184, 185, 187 |
| penguins, unidentified | ? | C | 137 |
| **Flying birds** | | | |
| Antarctic Fulmar *Fulmarus glacialoides* | P | P, O | 45, 98, 100, 119, 171 |
| Antarctic Petrel *Thalassoica antarctica* | P | P, O | 15, 45, 48, 49, 87, 98, 109, 122, 135 |
| Pintado Petrel *Daption capense* | ? | P, C | 45, 137 |
| Snow Petrel *Pagodroma nivea* | P | P, O, R, C | 17, 34, 45, 48, 56, 77, 78, 87, 98, 109, 135, 137, 140, 168, 171 |
| Wilson's Storm Petrel *Oceanites oceanicus* | P | P, O, C | 45, 78, 98, 137, 171 |
| petrels, unidentified | ? | O | 26 |
| **Mammals** | | | |
| Weddell Seal *Leptonychotes weddelli* | S, K | P, O | 21, 26, 34, 45, 78, 87, 119, 171 |
| Southern Elephant Seal *Mirounga leonina* | S | P | 45 |
| **Fish** | | | |
| *Pagothenia borchgrevinki* | ? | R | 92 |
| *Pagothenia* sp. | ? | P | 171 |
| *Pleuragramma antarcticum* | P | O, R | 34, 87, 92, 98, 184, 185, 188 |
| Liparidae | P | R | 84 |
| unidentified | P, S | O, F, P, R, C | 4, 45, 78, 92, 117, 137, 147, 171, 187 |
| **Invertebrates** | | | |
| unidentified | ? | R, F | 92 |
| mussels, unidentified | ? | R, F | 92 |
| polychaetes | P | P, R | 171 |
| amphipods | P | P, R | 171 |
| starfish, unidentified | ? | O | 187 |
| *Sterechinus* sp. | P | P, R | 171 |
| cephalopods, unidentified | P | ? | 185 |
| squid *Gonatus* sp. | ? | P | 98 |
| squid *Moroteuthis* sp. | ? | P | 98 |
| squid *Psychrotenthis* sp. | ? | P | 98 |
| krill *Euphausia* sp. | P | O | 34, 109 |
| **Other items** | | | |
| kitchen refuse, garbage | S | P, O, R | 21, 40, 47, 87, 92, 109, 168, 171, 172, 187 |

in the vicinity of skua nests, assuming that the skuas depended entirely on the Antarctic Petrel colony as a food source. Young (1994) surveyed a whole penguin colony and determined the number of penguin eggs and chicks that were lost to skuas. However, an earlier study (Young 1963b) found a high percentage of fish in the diet as well. Reinhardt (1995) ligatured chicks in order to get an estimate of the total food consumption. In contrast to results obtained from pellet collecting in the same geographical region (Peter *et al.* 1990, Pietz 1987, see Fig. 1) the composition found during the ligature study differed markedly with over 95% percent being marine food (excluding penguins) for the South Polar Skua, 2% for the Brown Skua, and 85% for mixed pairs. In comparison to theoretical considerations (Drent *et al.* 1992), however, the total food consumption is 3–4 fold underestimated by this method (Reinhardt 1998). Montalti *et al.* (1996) studied the stomach contents of adult South Polar Skuas. Although it was not clear whether birds were caught at random or when returning from a foraging trip, the figure obtained was similar to an average ligature sample in Reinhardt's (1997b) study.

## DISCUSSION

Furness (1987) reviewed the food of the Great Skua in the Northern Hemisphere, recording 99 food items and eggs from 14 species in the diet. As for the Great Skua, most of the Southern Hemisphere skuas feed on a wide variety of items, including eggs and chicks of penguins, flying birds, small mammals, fish, marine invertebrates, and garbage. In this review at least 111 prey species in the diet of skuas were recorded. This figure should be taken with caution since the

**TABLE 7**

**Food of different skua taxa during the breeding season at the Antarctic Peninsula, the South Shetland and South Orkney Islands. (SPS – South Polar Skua, MP – Mixed pair, BS – Brown Skua)**

| Food species | Foraging mode of | | | Sampling technique | Reference |
|---|---|---|---|---|---|
| | SPS | MP | BS | | |
| **Penguins** | | | | | |
| Adélie Penguin *Pygoscelis adeliae* | S? | ? | P, S | O, P, R | 5, 35, 102, 103, 115, 123, 149, 162, 163 |
| Chinstrap Penguin *P. antarctica* | | | P, S | O, P | 23, 111, 123, 162, 163 |
| Gentoo Penguin *P. papua* | | | P, S | O, P, R | 6, 35, 99, 111, 123, 162, 163 |
| penguin *Pygoscelis* sp. | ? | ? | P, S | O, P, R | 57, 112, 115, 123 |
| **Flying birds** | | | | | |
| Southern Giant Petrel *Macronectes giganteus* | ? | | P | ?, O | 24, 111, 116 |
| Pintado Petrel *Daption capense* | P | | P | P, O | 105, 111, 116, 175 |
| Snow Petrel *Pagodroma nivea* | | | P | ? | 20 |
| Antarctic Prion *Pachyptila desolata* | S | | P | ? | 20, 57, 115 |
| prion *Pachyptila* sp. | | | P | P | 7 |
| Black-bellied Storm Petrel *Fregetta tropica* | P | | P | P, R | 51, 94, 123 |
| Wilson's Storm Petrel *Oceanites oceanicus* | P, S | ? | P | P | 20, 51, 57, 111, 115, 123, 136 |
| Black-necked Swan *Cygnus melanocorypha* | S | | S | O | 74 |
| Imperial Cormorant *Phalacrocorax atriceps* | P | | | O | 5 |
| Kelp Gull *Larus dominicanus* | P | | ? | O, P | 81, 111, 115, 123 |
| Antarctic Tern *Sterna vittata* | P | | P | O, P | 8, 73, 111, 115, 123 |
| **Mammals** | | | | | |
| baleen whale, unidentified | | | S | O | 113 |
| Southern Elephant Seal *Mirounga leonina* | | | S | O | 113, 38 |
| Weddell Seal *Leptonychotes weddelli* | | | S | O | 111 |
| Antarctic Fur Seal *Arctocephalus gazella* | | | S | P, R | 123 |
| **Fish** | | | | | |
| *Pleuragramma antarcticum* | P | | | R, C | 57, 85, 115, 123 |
| *Pleuragramma* sp. | P | P | P | R | 111 |
| *Electrona antarctica* | P | P | | R, C | 85, 123 |
| *E. carlsbergi* | P | | | C | 85 |
| *Trematomus newnesi* | ? | | | C | 123 |
| *Krefftichthys anderssoni* | P | | | C | 85 |
| *Chamsocephalus aceratus* | P | | | C | 85 |
| *Gymnoscopelus braueri* | P | | | C | 85 |
| *Protomyctophum normani* | P | | | C | 85 |
| *P. tenisoni* | P | | | C | 85 |
| unidentified | K, P | P | ? | O, R | 19, 20, 80, 102, 104, 105, 112, 115 |
| **Invertebrates** | | | | | |
| *Branchinecta* sp. | P | | P | O | 52, 115 |
| Antarctic Krill *Euphausia superba* | P, S | | ? | O, P, R | 57, 99, 102, 115, 123 |
| *Eurythenes gryllus* | ? | | ? | R | 121, 123 |
| *Themisto gaudichaudii* | P | | | C | 85 |
| *Pontogeneia antarctica* | P | | | C | 85 |
| amphipods, unidentified* | P | | | R | 111, 123 |
| *Sterechinus neumayeri* | | | ? | P | 111 |
| *Nacella concinna* | | | ? | R | 123 |
| *Patinigera polaris* | ? | | | P | 111 |
| **Other items** | | | | | |
| station garbage | S | S | S, K | O, P, R | 5, 23, 102, 111, 112, 115, 123 |

* The amphipod species mentioned in Reinhardt (1995) have been identified to species level by M. Rauschert. The category 'amphipods' would subsequently break down into nine species categories.

number of food items will increase with an identification to a lower taxonomic level (e.g. amphipods and fish). This holds also true for kitchen refuse. When skuas use this resource they virtually feed on everything including soap, cigarettes, pasta, vegetables and salads (e.g. Stonehouse 1956, Peter *et al.* 1988, Wang & Norman 1993, Reinhardt 1995). Throughout the literature, cannibalism is not frequently recorded and was thus ignored in this study. However, it is supposed to be very common and even one of the main reasons for breeding failure (Reinhardt 1995). It has mainly reported from South Polar Skuas and Brown Skuas (Pietz 1987, Mougeot *et al.* 1998, Z. Wang pers. comm.)

Contrary to common statements that skuas are opportunistic feeders, Moncorps *et al.* (1998) and Mougeot *et al.* (1998) provided evidence that this is not necessarily the case. Young (1978) showed that Brown Skuas on the Chatham Islands do not prey upon all the species found within the breeding area. From the present study it appears that skuas rarely prey or scavenge upon Pintado or Cape Petrels *Daption capense* or the Pale-faced (Greater) *Chionis alba* and Black-faced (Lesser) Sheathbills *C. minor*. Since skuas usually have easy access to these species, other reasons must account for their avoidance of these prey (Weidinger 1998). Another interesting case of differential predation was given by Hahn & Quillfeldt (1998). They showed that skuas preyed about 1.68 times more often on Black-bellied Storm Petrel than on Wilson's Storm Petrel although the latter was 4.4 times more abundant. This indicates a 7.4 times higher predation pressure upon Black-bellied Storm Petrel possibly based on easier availability. All these example show that prey selectivity may be more common among skuas than previously assumed.

This study presents food items separately for skua taxa, as well as for regions. Figure 1 shows a high diet similarity across the taxa, although there might be some bias in the data as e.g. from Young's (1994) intensive studies no frequency distribution of diet could be derived. The diets are apparently more influenced by ecological conditions than by taxonomy. Brown Skua diets around Marion, Crozet and the Kerguelen Islands are more similar to those of the Tristan or the South Polar Skua on the continent than to the Brown Skua diet of the Antarctic Peninsula. In the East Atlantic and Pacific part of the Southern Ocean, skua diet is generally dominated by non-penguin bird species and small mammals, although more quantitative data are needed. This may, in part be dependent on the skua's foraging behaviour. So far, nocturnal foraging has only been recorded from the Chatham Islands (Young *et al.* 1978) and the Kerguelen group (Mougeot *et al.* 1998). Its occurrence in different regions has not been proved. However, the occurence of Wilson's and Black-bellied Storm Petrels in the diet of skuas on the South Shetlands (e.g. Peter *et al.*1988, Myrcha 1992, Hahn & Quillfeldt 1998) points toward the possibility that individual, often specialized pairs (Osborne 1985) might hunt at dusk or at night. Pietz (1986) found the lowest activity level of both South Polar and Brown Skua in the hours of darkness, when also the lowest proportion of food was delivered to the chicks (Reinhardt 1997b).

As found in several studies (Peter *et al.* 1990, Pietz 1987, Reinhardt 1995, Reinhardt *et al.* 1998), the literature reviewed here shows a difference in the diets of Brown and South Polar Skua in region 5 (Table 7). The food items that are shared are sometimes obtained by predation by one of the skua taxa and by scavenging (or the origin is unknown) by the other (Table 7). There is still some debate on whether the relationship between the two taxa is governed by competition. South Polar Skuas feed on fish and penguins in continental Antarctica (Table 6) but feed mainly on fish in the zone of overlap with the Brown Skua (Fig. 1). The Brown Skua is thought to monopolize the penguin food resource (e.g. Pietz 1987). This could be seen as competition. However, the dominance of fish in the South Polar Skua diet in the Antarctic Peninsula region (Pietz 1987, Peter *et al.* 1990, Reinhardt 1995, Montalti *et al.* 1996) can also be explained as their first preference. In continental Antarctica, isolation from fish by frozen surrounding waters and subsequent increased travel costs could have led to the use of penguins as a secondary food. Although no older data exist for comparison, the present intensive use of fish by the South Polar Skua is paralleled by a northward range expanding of the South Polar Skua as far north as the South Orkney Islands (Hemmings 1984). This was hypothesized to be linked with an increase in the abundance of krill and its predators, as e.g the fish species *Electrona antarctica* and *Pleuragramma antarcticum* (Hemmings 1984). Investigations either from other areas of sympatric breeding of two different skua forms (Balleny Islands, Patagonian coast) or from long-term diet studies of the South Polar Skua could help to illuminate this problem.

Apart from the need of further quantitative studies we would like to focus on a few further problems. Reinhardt (1998) found a discrepancy between ligature results and theoretical energetic values (Drent *et al.* 1992). He could not completely solve the problem whether this was largely the problem of the theory or of the technique employed. Furthermore, there are still no data on whether adult birds have the same diet as their chicks. Most of the studies focus, either direct or indirect, on food that is associated with chick feeding. Finally, except for the attempts by Mougeot *et al*. (1998) there seem to be no data on potential seasonal fluctuations of the diet. Skuas should represent ideal study organisms in order to find out whether chick diet reflects the chicks' nutritional needs or just the adults' catch.

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