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Diet of the brown skua *Catharacta skua lönnbergi* on the Kerguelen archipelago: comparisons between techniques and between islands

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Abstract The diet of the brown skua *Catharacta skua lönnbergi* was studied on the Kerguelen archipelago, during the chick-rearing period, over four breeding seasons (1987/1988, 1990/1991, 1992/1993 and 1993/1994). Prey remains and regurgitated pellets left by the breeding pairs were analysed and compared between two nearby and similar islands that mainly differ according to the presence or absence of the rabbit, since its eradication from one of them in 1992. Proportions of prey in diets varied between sampling methods (remains/pellets), localities, years, breeding territories, breeding pairs and non-breeding individuals. The brown skua preyed upon few species of burrowing petrels and mainly on the blue petrel. Rabbits were exploited secondarily although they apparently reduced the predation pressure on the blue petrel. The eradication of rabbits from one of the islands, during a restoration programme, has not basically changed the trophic interactions between brown skuas and petrels.

Introduction

The diets of skuas (*Catharacta* and *Stercorarius*) are remarkably diversified in the different localities where they breed (reviews in Furness 1987). This is partly related to their diverse feeding techniques, i.e. aerial or

terrestrial hunting, fishing, scavenging and kleptoparasitism, which allow skuas to exploit a wide range of resources, and categorise them as typical opportunistic feeders (Eklund 1961; Le Morvan et al. 1967; Young 1978; Osborne 1985; Furness 1987; Ryan and Moloney 1991). On subantarctic islands, the brown skua *Catharacta skua lönnbergi* feeds mainly on penguins and/or petrels (Young 1978; Moors 1980; Sinclair 1980; Adams 1982; Osborne 1985; Pietz 1987). However, they are also known to prey upon introduced mammals, i.e. the black rat *Rattus rattus* on Crozet archipelago (Barré 1976; Stahl and Mougín 1986) and the rabbit *Oryctolagus cuniculus* on Macquarie Island (Johnston 1973; Jones and Skira 1979; Skira 1984). Although rabbit predation has already been noted on Kerguelen archipelago (Lésel and Derenne 1975; Boussès 1991, Chapuis et al. 1994a), no study has yet assessed their part in the diet of skuas. Moreover, incidence of prey in diet of skuas has been widely used as an indicator of prey abundance but this has rarely been tested, nor were compared diets of breeders and non-breeders, and the sampling techniques used, i.e. pellets and remains (Young 1978; Furness 1979; Jones 1980; Moors 1980; Adams 1982; Schramm 1983; Fraser 1984; Osborne 1985; Stahl and Mougín 1986; Ryan and Moloney 1991; Mund and Miller 1995).

We therefore investigated the diet of the brown skua on Kerguelen archipelago between 1987 and 1994, in situations where skuas could feed, or not, on an introduced mammal, the rabbit. The study was conducted during the chick-rearing period, on two islands that were strongly affected by the presence of rabbits (Chapuis et al. 1994a). Following a restoration programme on Kerguelen archipelago (Chapuis 1995; Chapuis et al. 1995), rabbits were eradicated in July–August 1992 from one of the studied islands (Chapuis and Barnaud 1995) and prey stocks were estimated. The similarities offered by these two islands, in terms of vegetation and petrel communities, therefore provided an opportunity to compare the diet of the brown skua in the presence and absence of rabbits with other factors being equal. The

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consequences of rabbit removal in the skuas-petrels trophic relationships could thus be assessed. We also compared diets according to sampling methodology (remains vs pellets), territories and breeding status (breeding pairs vs non-breeding individuals).

Materials and methods

Study sites

The Kerguelen archipelago (48°25–50°S, 68°25–70°35E) is composed of a main island (6,500 km²) and about 100 smaller islands (1–200 km²). This study was conducted on two islands of this archipelago, Cimetière Island (3.1 km²) and Verte Island (1.5 km²), both located within the Morbihan Gulf (Fig. 1). These two islands, 2 km apart, present similar plant communities that were both damaged by rabbits whose impact has led to a reduction of vascular plant species diversity and biomass, e.g. scarcity of the Kerguelen cabbage *Pringlea antiscorbutica* or *Azorella selago* being replaced by *Acaena magellanica* (Léssel and Derenne 1975; Chapuis and Boussès 1989).

The prey

The two islands are characterised by similar burrowing petrel communities and the absence of penguin colonies. Verte Island was estimated to shelter more than 70,000 pairs of petrels in 1992/1993. Among them, blue petrels (*Halobaena caerulea*: 36,000 pairs), Antarctic prions (*Pachyptila desolata*: 27,000 pairs) and South Georgian diving petrels (*Pelecanoides georgicus*: 10,000 pairs) were the most numerous (V. Bretagnolle, unpublished data). Cimetière Island, twice the area of Verte Island, shelters a higher density of brown skuas (6.5 pairs · km⁻² vs 3.3 pairs · km⁻²) and is presumably occupied by a larger population of petrels.

Rabbits were introduced in 1874 on the main island and afterwards on eight other islands (1.4–40 km²) including Verte and

Cimetière Islands (Chapuis et al. 1994a). Rabbit density was comparable between the two islands, although precisely estimated at 8 ind · ha⁻¹ on Verte Island before its eradication in 1992 (Chapuis and Barnaud 1995).

The brown skua

The breeding population of brown skua is between 2,000 and 4,000 pairs, distributed all over the archipelago (Weimerskirch et al. 1989). The density of breeding pairs is higher on islands and areas that are not occupied by introduced cats (*Felis catus*), probably because numerous colonies of burrowing petrels are nesting there, or near abundant colonies of penguins (*Aptenodytes forsteri*, *Eudyptes chrysolophus* and *E. chrysocome*). Five pairs were successfully breeding on Verte Island in 1992–1993 and 1993–1994. About 20 breeding pairs and a club of ca. 50 non-breeding individuals were present each year on Cimetière Island during the period 1987–1994.

The breeding cycle of the brown skua on Kerguelen archipelago appears to be synchronised with those of the blue petrel and the South Georgian diving petrel, but less so with that of the Antarctic prion (Fig. 2). The breeding season of the brown skua also occurs during the birth period of the rabbit (Fig. 2).

Methods

Diet of brown skua was assessed by two different methods: (1) identification of prey remains, and (2) examination of regurgitated pellets. Both materials were collected in January, over several breeding seasons, in the proximity of nests of breeding pairs on Verte and Cimetière Islands (see Table 1 for sample sizes). During the breeding season 1993/1994, 92 pellets found at the club at Cimetière Island were also collected.

Species identification from prey remains was based on wing lengths and biometric characteristics of the skull. Wings collected were sometimes still connected to the sternum, but more often were separated. In this case, they were first sorted out by species, and then pairs were arbitrarily reconstituted with a left and a right wing. Each isolated remaining wing was counted as an additional prey. For rabbit remains, only skulls were counted. Pellet contents were analysed according to the presence of bone fragments, feathers and hairs. Petrel species were identified from their skulls, tarsus length and bill characteristics. In most cases however, only tarsi were available. As tarsus length of blue petrels and Antarctic prions were similar (34.0 ± 0.9 mm, min: 33.1, max: 37.2, and 33.6 ± 1.1 mm, min: 31.0, max: 35.8 for 374 blue petrels and 128 Antarctic prions respectively), we pooled these 2 species in our analyses.

Results are expressed in relative abundance (prey remains) and frequency of occurrence (pellets). Indeterminate items were removed from analyses (1.0% for prey remains and 14.4% for pellets). In order to compare remains and pellets results, we used Student's *t*-tests for matched samples. We used the *G*-test for comparing pellets of the breeding pairs on each island in 1992/1993 and 1993/1994. One-way ANOVAs were performed to analyse the interannual variations in prey remains (data were arcsine transformed) on Cimetière Island. A posteriori Scheffé's comparison tests were then used to identify years that were accounting for the difference found. In a combined analysis, we also tested for possible effects of both year and locality using two-way ANOVAs. These were performed separately for diets assessed from prey remains and regurgitated pellets (data arcsine transformed). In order to know if rabbits changed the relative proportions of each petrel species in the diet of skuas, one-way and two-way ANOVAs were also performed by removing data on rabbits. Lastly, the chi-square test was used to compare pellets of breeding pairs with those of non-breeding individuals.

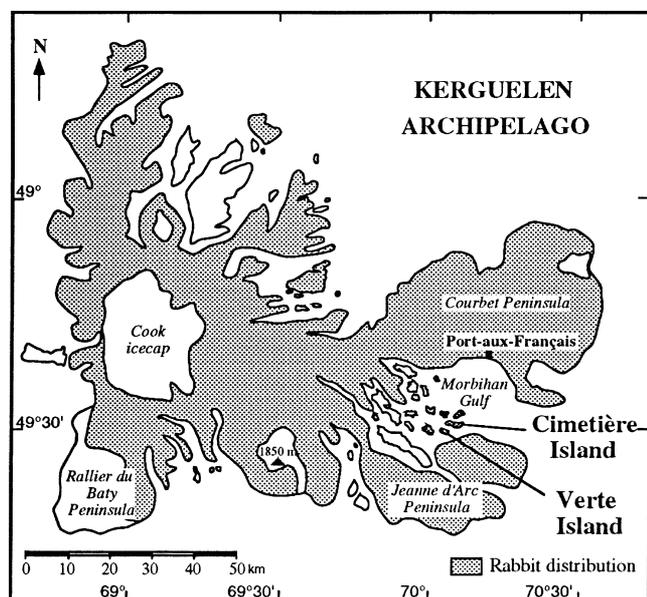


Fig. 1 Location of Cimetière and Verte Islands, and rabbit distribution (from Boussès 1991) in the Kerguelen archipelago

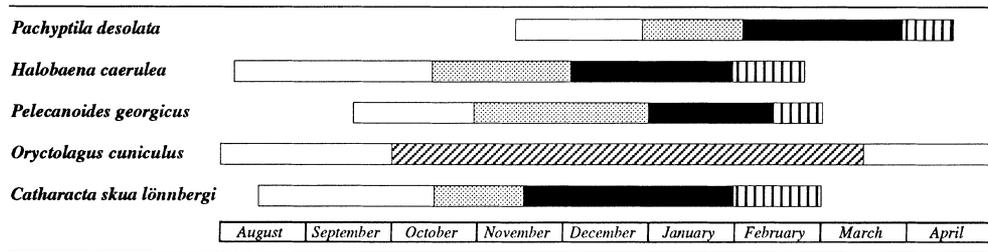


Fig. 2 Breeding stages of the brown skua and petrels on the Kerguelen archipelago (from Weimerskirch et al. 1989; and personal observations): return on territory (*white*), laying and incubation (*grey*), hatching and chick rearing (*black*), fledging (*hatching*). For the rabbit, only the birth period is indicated (from Boussès 1991). Data are presented per fortnight

Table 1 Numbers of prey remains and pellets collected during different breeding seasons of the brown skua on Verte and Cimetière Islands (*n* numbers of sampled breeding pairs)

Breeding seasons	Verte Island		Cimetière Island	
	Remains	Pellets	Remains	Pellets
1987/1988	–	–	664 (<i>n</i> = 9)	–
1990/1991	–	–	231 (<i>n</i> = 4)	–
1992/1993	757 (<i>n</i> = 5)	231 (<i>n</i> = 5)	526 (<i>n</i> = 9)	327 (<i>n</i> = 10)
1993/1994	797 (<i>n</i> = 5)	150 (<i>n</i> = 5)	597 (<i>n</i> = 9)	473 (<i>n</i> = 10)
Total	1554	381	2018	800

Table 2 Relative abundance (% ± standard deviation) of prey species in brown skua remains during chick rearing period on Verte and Cimetière Islands per breeding season (*n* numbers of sampled breeding pairs)

	Breeding seasons				Average
	1987/1988 (<i>n</i> = 9)	1990/1991 (<i>n</i> = 4)	1992/1993 (<i>n</i> = 9)	1993/1994 (<i>n</i> = 9)	
Cimetière Island					
<i>Halobaena caerulea</i>	80.3 ± 6.0	82.7 ± 8.5	77.5 ± 9.8	89.6 ± 8.1	82.5 ± 9.2
<i>Pachyptila desolata</i>	7.7 ± 1.8	2.7 ± 1.9	8.9 ± 7.4	7.0 ± 6.4	7.2 ± 5.5
<i>Pelecanoides georgicus</i>	6.8 ± 4.9	3.1 ± 2.8	3.4 ± 2.8	2.7 ± 3.8	4.2 ± 4.0
<i>Oryctolagus cuniculus</i>	3.7 ± 2.8	10.7 ± 12.2	8.5 ± 6.9	0.4 ± 0.9	5.0 ± 6.7
Other prey	1.5 ± 1.5	0.8 ± 1.6	1.7 ± 2.6	0.3 ± 0.8	1.1 ± 1.8
Mean number of remains	73.8 ± 24.5	57.8 ± 27.3	58.4 ± 31.1	66.3 ± 26.1	65.1 ± 26.8
Verte Island					
<i>Halobaena caerulea</i>			86.4 ± 7.1	90.4 ± 3.3	88.4 ± 5.6
<i>Pachyptila desolata</i>			4.4 ± 4.2	4.8 ± 2.0	4.6 ± 3.1
<i>Pelecanoides georgicus</i>			7.9 ± 3.1	4.1 ± 2.4	6.0 ± 3.3
Other prey			1.3 ± 1.1	0.7 ± 0.8	1.0 ± 0.4
Mean number of remains			151.4 ± 88.2	159.4 ± 37.7	155.4 ± 64.1

Results

Incidence of prey in diets and comparison between methods of collect

The diet of the brown skua appeared to be mainly composed of three burrowing petrels on the two islands, and additionally, rabbits on Cimetière Island. Blue petrel remains accounted for more than 80% of all prey, followed by Antarctic prions, South Georgian diving petrels and rabbits on Cimetière Island (Table 2). Other minor prey included *Pterodroma lessonii*, *Pterodroma*

macroptera, *Lugensa brevirostris*, *Sterna virgata*, *Anas aetoni* and *Phalacrocorax atriceps*.

The analysis using pellets gave similar results, although the percentages of species differed (Table 3). Following the rabbit eradication in 1992, no prey remain of this species was found on Verte Island in the two consecutive breeding seasons (1992/1993 and 1993/1994) but its presence in pellets was certainly due to scavenging on dead animals and/or capture of individuals on a nearby island.

Thus, we found significant differences between the two methods used for assessing diet of the brown skua, with the proportion of blue petrel and Antarctic prion

Table 3 Frequency of occurrence (% \pm standard deviation) of prey species in brown skua pellets during chick-rearing period on Verte and Cimeti re Islands per breeding season (n numbers of sampled breeding pairs)

	Breeding seasons		
	1992/1993 ($n = 10$)	1993/1994 ($n = 10$)	Average
Cimeti�re Island			
<i>Halobaena caerulea-Pachyptila desolata</i>	59.0 \pm 16.1	64.4 \pm 13.5	61.7 \pm 14.8
<i>Pelecanoides georgicus</i>	15.9 \pm 11.0	15.1 \pm 8.3	15.5 \pm 9.5
<i>Oryctolagus cuniculus</i>	29.5 \pm 14.4	24.6 \pm 12.2	27.1 \pm 13.2
Mean number of pellets	32.7 \pm 23.4	47.3 \pm 25.9	40.0 \pm 25.2
Verte Island			
	($n = 5$)	($n = 5$)	
<i>Halobaena caerulea-Pachyptila desolata</i>	76.3 \pm 8.9	77.5 \pm 7.5	76.9 \pm 7.8
<i>Pelecanoides georgicus</i>	24.1 \pm 11.7	19.4 \pm 5.8	21.7 \pm 9.0
<i>Oryctolagus cuniculus</i>	2.1 \pm 2.3	0.5 \pm 1.2	1.3 \pm 1.9
Mean number of pellets	46.2 \pm 15.6	30.0 \pm 18.9	38.1 \pm 18.4

being significantly lower in pellets than in remains ($t = 8.85$, $df = 26$, $P < 0.001$), while South Georgian diving petrel and rabbit proportions were higher accordingly ($t = 7.62$ and $t = 5.75$, $df = 26$, $P < 0.001$, respectively).

Interannual variation

Using prey remains collected on Cimeti re Island, we found that proportions of blue petrel (one-way ANOVA, $F_{3,27} = 3.83$, $P < 0.05$) and rabbit ($F_{3,27} = 5.23$, $P < 0.01$) varied significantly with year (Table 2). Using a posteriori Scheff 's comparison tests, we found that this difference was actually accounted for by the comparison between years 1993/1994 and 1992/1993 ($P < 0.05$) where blue petrel occurred at higher proportions and rabbit at lower proportions in remains of the former year 1993/1994 (Table 2). Relative abundance of Antarctic prion ($F_{3,27} = 1.14$, $P = 0.35$), South Georgian diving petrel ($F_{3,27} = 1.90$, $P = 0.15$) and other prey ($F_{3,27} = 1.68$, $p = 0.19$) did not vary significantly across breeding seasons (Table 2). It should be further noted that when rabbit remains were removed from analyses, no effect of year was apparent for any other prey category (blue petrel: $F_{3,27} = 1.96$, $P = 0.14$; Antarctic prion: $F_{3,27} = 1.13$, $P = 0.36$; South Georgian diving petrel: $F_{3,27} = 1.93$, $P = 0.15$; other prey: $F_{3,27} = 1.71$, $P = 0.19$).

Between-island comparisons

As breeding season had a significant effect on the proportions of the different prey items (see above), we carried out a two-way analysis with year and locality as factors. Using prey remains, the blue petrel's incidence varied significantly with breeding season, as did that of the South Georgian diving petrel with locality (Table 4). However, when relative abundances of each prey category were calculated without rabbits, no significant dif-

ferences were found except for the South Georgian diving petrel that was still accounting for higher proportions in prey remains collected on Verte Island (Table 4). In order to compare these results when pellets were analysed, we carried out an ANOVA with proportions of blue petrel and Antarctic prion gathered: no difference was detected between islands ($F_{1,24} = 0.08$, $P = 0.78$), but their incidence was higher in 1993/1994 than in 1992/1993 ($F_{1,24} = 12.73$, $P < 0.01$). However, frequency of occurrence of blue petrel-Antarctic prion was higher in pellets collected on Verte than on Cimeti re Island, but did not differ with breeding seasons (Table 4). Proportions of South Georgian diving petrel did not vary significantly between islands or across years (Table 4).

Variations between pairs, and between breeding and non-breeding individuals

On Cimeti re Island, prey remains differed significantly between the breeding pairs (Fig. 3; G -test, $G = 49.61$ and $G = 52.35$, $df = 18$, $P < 0.001$ for 1992/1993 and 1993/1994 respectively). Analyses performed on each prey category further revealed that diets differed significantly for each of them ($G > 21.92$, $df = 18$, $P < 0.01$). Results for Verte Island yielded slightly different results, with significant variations only found in 1992/1993 (Fig. 3; $G = 14.43$, $df = 4$, $P < 0.01$), for the South Georgian diving petrel ($G = 16.27$, $P < 0.01$) but not for the blue petrel-Antarctic prion category ($G = 8.37$, $P = 0.08$).

Diet of non-breeding individuals from Cimeti re Island (1993/1994), determined from regurgitated pellets, was composed by 41.3% of blue petrel-Antarctic prion, 34.8% of South Georgian diving petrel and 20.7% of

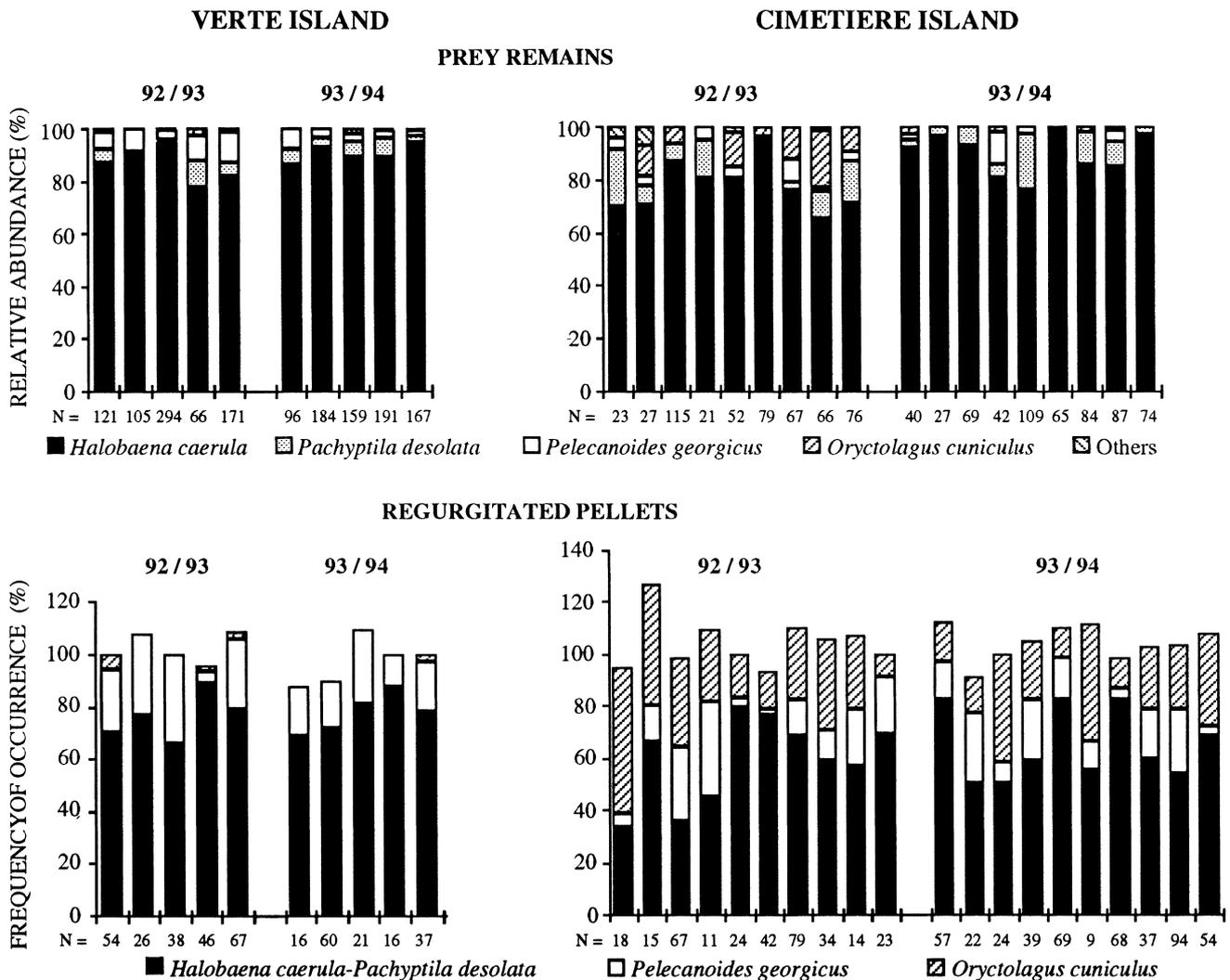
Fig. 3 Diets of brown skua breeding pairs on Verte and Cimeti re Islands during chick-rearing period, in the 1992/1993 and 1993/1994 breeding seasons, determined from prey remains and regurgitated pellets. Each *histogram* corresponds to a breeding pair

Table 4 Results of two-way ANOVAs (F values) of the effects of locality and year on diets of brown skua of the Kerguelen archipelago. ANOVAs were performed on prey remains (I) including

data on rabbit and (2) after the removal of data on rabbit, and on pellets (Hc *Halobaena caerulea*; Pd *Pachyptila desolata*; Pg *Pelecanoides georgicus*; Oc *Oryctolagus cuniculus*)

Prey remains (1)						
Factor	df	Hc	Pd	Pg	Oc	Other prey
Locality (Cimetière, Verte)	1	0.95	0.90	6.47*	12.73**	0.02
Year (92/93, 93/94)	1	5.59*	0.03	2.63	7.99**	2.71
Locality \times Year	1	1.61	0.29	0.24	7.99**	0.25
Residual	24					
Prey remains (2)						
Factor	df	Hc	Pd	Pg	Oc	Other prey
Locality (Cimetière, Verte)	1	0.03	1.08	5.73*	–	0.82
Year (92/93, 93/94)	1	1.49	0.00	2.86	–	2.79
Locality \times Year	1	0.05	0.40	0.15	–	0.31
Residual	24					
Pellets						
Factor	df	Hc-Pd	Pg	Oc		
Locality (Cimetière, Verte)	1	8.86**	2.70	75.73**		
Year (92/93, 93/94)	1	0.41	0.18	1.58		
Locality \times Year	1	0.18	0.14	0.05		
Residual	26					

* $P < 0.05$; ** $P < 0.01$



rabbit. Compared to the diet of breeding pairs in the same year, pellets of birds from the club thus contained significantly less blue petrel-Antarctic prion ($\chi^2_1 = 5.43$, $P < 0.05$), more South Georgian diving-petrel ($\chi^2_1 = 11.27$, $P < 0.001$), and there was equal occurrence of rabbit ($\chi^2_1 = 0.0004$, $P = 0.98$).

Discussion

Incidence of prey categories was found to differ according to the sampling technique that was used (i.e. prey remains vs regurgitated pellets). Although prey are usually carried back to the nest where remains are left on the ground, small petrels such as diving or storm petrels are likely to be swallowed whole (Young 1978; Sinclair 1980; Fraser 1984; Osborne 1985; Ryan and Moloney 1991). Similarly, other studies on Macquarie Island revealed that brown skuas kill mainly young rabbits (Johnston 1973; Jones and Skira 1979), which are easier to catch than adults, and could also be swallowed whole. Presumably, some young rabbits are not carried back to the nest as they are too heavy for the skuas, which could also apply for the few sick subadult and adult rabbits caught that are infected with myxoma virus (Selkirk et al. 1990), a virus that was introduced in 1955–1956 in the Kerguelen archipelago (Chapuis et al. 1994b). This probably explains why South Georgian diving petrels, or rabbits, are better represented in pellets than in remains (see also Fraser 1984; Ryan and Moloney 1991).

We also found that the incidence of small prey in remains was higher on Verte than on Cimetière Island. Breeding pairs of brown skua vigorously defend a feeding territory against any intruder with long-call displays or aerial chases and attacks (Furness 1987). Trivelpiece et al. (1980) showed that territorial brown skuas had significantly more agonistic interactions with non-territorial conspecifics than with other territorial pairs, the former being the principal food competitors. Similar observations of intrusions within territories, conflicts for food or kleptoparasitism between conspecifics have been made on brown skuas (Barré 1976; Sinclair 1980; F. Mougeot, F. Genevois and V. Bretagnolle, unpublished work), South polar skuas *Catharacta maccormicki* (Young 1963; Le Morvan et al. 1967), Tristan skuas *Catharacta skua hamiltoni* (Furness 1987) and great skuas *Catharacta skua skua* (Bayes et al. 1964; Furness 1987). Owing to the presence of a club of non-territorial skuas on Cimetière Island, breeding pairs might be more subject to feeding competition than those of Verte Island. Thus, skuas on Cimetière Island, in order to avoid being robbed, may swallow their prey whole more frequently than those of Verte Island. This may account for lower proportions of South Georgian diving petrel remains around nests on Cimetière Island, while we found no differences with regard to pellets.

Feeding competition may also explain the differences found in pellets between breeding pairs and non-breed-

ing individuals, with the latter showing a higher proportion of South Georgian diving petrels and significantly less blue petrels and Antarctic prions. While agonistic interactions between breeding pairs are infrequent (Trivelpiece et al. 1980), non-territorial skuas are more likely to be affected by intra-specific kleptoparasitism as they do not own feeding territories (Ryan and Moloney 1991). They may therefore select smaller prey items, such as diving petrels, that they could swallow whole (Ryan and Moloney 1991). It is also possible that their hunting success on larger prey such as blue petrels or Antarctic prions is lower compared to that of breeding birds that can hunt in pairs (Ryan and Moloney 1991). Lastly, this club is found on bare soils, with poor plant cover, i.e. the habitat of South Georgian diving petrels (Weimerskirch et al. 1989).

There is an overall disagreement between relative frequencies of prey categories, either remains or pellets, and relative abundance of burrowing petrels on Verte Island (Table 5). This tends to suggest that brown skuas are selective in their diet, a result that was found also at Prince Edward Island (Adams 1982), Chatham Islands (Young 1978), Inaccessible Island (Fraser 1984; Ryan and Moloney 1991), Gough Island (Furness 1987), and another locality at Kerguelen (F. Mougeot, F. Genevois and V. Bretagnolle, unpublished work). Actually, the brown skua appears to be highly selective towards the blue petrel. Compared to other petrel species, this high predation level may be linked to the greater abundance of the blue petrel, the synchronisation of its breeding cycle to that of the brown skua, and its morphology that may maximise the ratio between energetic benefit and cost of capture. The late breeding cycle of the Antarctic prion and the small size of the South Georgian diving petrel may be responsible for their lower representation in diet, although they may also be more difficult to catch. The breeding pairs defend feeding territories, where they exploit available resources, which may also lead to local diet specialisation (Jones and Skira 1979; Moors 1980; Sinclair 1980; Adams 1982; Osborne 1985). This territory specialisation was found on Cimetière Island, but less so on Verte Island, although in the latter case we sampled a smaller number of pairs. Verte Island is also smaller in size, and thus slightly less diverse in terms of habitats.

Table 5 Relative abundance of burrowing petrels on Verte Island in 1992/1993, compared to their incidence in brown skua diet either obtained from prey remains or regurgitated pellets

Species	Relative abundance (%)	Diet of brown skuas (%)	
		Remains	Pellets
<i>Halobaena caerulea</i> (Hc)	49.3	86.4	
<i>Pachyptila desolata</i> (Pd)	37.0	4.4	
Hc and Pd	86.3	90.8	76.3
<i>Pelecanoides georgicus</i>	13.7	7.9	24.1

Diet of breeding pairs was generally stable over years, except for the 1993/1994 breeding season where the relative abundance of the blue petrel in prey remains was higher compared to other years, especially on Cimetière Island. This difference may have resulted from a decrease in rabbit density, as no variation in other prey categories was significant when rabbit remains were excluded from the analyses. It suggests that the presence of rabbits on the island reduces the predation pressure of skuas on blue petrels, as observed with other petrels on Macquarie Island (Moors 1980). This is also suggested by the comparison between islands, where the presence of rabbits on Cimetière Island results in a significant decrease of blue petrel captures, which confirm the occurrence of a relationship between rabbit and blue petrel predation levels. However, this relationship was found in pellets but not in remains, because of the underestimated incidence of rabbits in the latter.

In conclusion, this study has shown that analysing diet on the basis of remains or pellets, as well as sampling breeding or non-breeding birds, may provide different results. It also showed that the diet of the brown skua is a poor indicator of the relative abundance of its prey (see also Ryan and Moloney 1991; F. Mougeot, F. Genevois and V. Bretagnolle, unpublished work). Lastly, we have shown that rabbit constitutes a secondary prey item for brown skuas on the Kerguelen archipelago but that its presence reduces the predation on the blue petrel. Because Verte and Cimetière Islands, in particular, were damaged by the presence of rabbits that strongly modified plant communities by grazing, digging and trampling, further inducing a strong erosion process (Chapuis et al. 1994a), a restoration program eventually took place on Verte Island. Rabbits are also responsible for the destruction of breeding sites for several petrels (e.g. blue petrel and Antarctic prion: Weimerskirch et al. 1989). Mayes Island (2.3 km²), another island of the Morbihan Gulf, characterised by the absence of alien herbivorous mammals, holds ca. 80–100 breeding pairs of brown skua (F. Mougeot, F. Genevois and V. Bretagnolle, unpublished work). The extirpation of rabbits on Verte Island in 1992 did not change the number of breeding brown skuas, at least until 1996, probably because rabbits were exploited secondarily by skuas. Furthermore, this restoration programme constitutes a privileged way to regenerate original plant communities (Chapuis, 1995; Chapuis and Barnaud, 1995), which may lead to the recolonisation of new sites by petrels and a subsequent increase in the number of brown skuas.

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