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Predation on burrowing petrels by the brown skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen

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Abstract

The diet of the brown skua (*Catharacta skua lönnbergi*) was studied at Mayes Island, Kerguelen archipelago, by collection of prey remains on 11 territories during the complete breeding cycle of the species there. In nine territories, collections were daily or every two days for a quantitative investigation of the diet. The blue petrel (*Halobaena caerulea*) and thin-billed prion (*Pachyptila belcheri*) accounted for, respectively, 72.9 and 19% of the remains. Differences in diet and prey capture rate were analysed according to territory size, local abundance of prey inferred from the vegetation cover of territories, colony attendance patterns of prey, and according to the breeding timing and success of skuas. Skuas holding large territories caught more prey, and especially more blue petrels than those with small territories. Diet reflected local abundance of blue petrel and thin-billed prion but the blue petrel was apparently preferred to other available prey. Failure to breed was not significantly related to hunting performance of the skua or to food availability, but sample size was small. Variations over time of prey capture rates reflected the colony attendance patterns of the main prey. Captures of blue petrel and thin-billed prion were most numerous during their respective laying, incubation and hatching periods, decreasing during chick-rearing. Prey capture rates were greatest when brown skuas were hatching, and decreased during chick-rearing to a minimum when young skuas were fledged. Capture rate patterns differed according to laying date of skuas: early breeding skuas caught more prey and were well synchronized with the breeding cycle of the blue petrel and late breeders exhibited more dependence on the thin-billed prion for some periods. Finally, this study has allowed us to assess the impact of the brown skuas upon the burrowing petrels on this locality.

Key words: predation, brown skua, petrels

INTRODUCTION

The brown skua (*Catharacta skua lönnbergi*) has a wide circumpolar breeding range, which includes most of the southern ocean islands from the Southern Antarctic Peninsula to Chatham Island (Furness, 1987). It is migratory, spending the summer on the breeding colonies, and then dispersing at sea northward to about 10 in winter. In some localities, however, where prey are available year-round, it may be resident (Hemmings, 1986). *Catharacta* skuas in general have a remarkably diverse range of feeding methods: active predation on penguins (Young, 1994), burrowing petrels (Young, 1978; Jones, 1980; Moors, 1980; Adams, 1982; Fraser, 1984; Green, 1986; Stahl & Mougin, 1986; Wang Zipan & Norman, 1993), or other seabirds (Furness, 1981), scavenging dead mammals, birds, intertidal marine invertebrates or human refuse (Trivelpiece, Butler & Volkman, 1980; Stahl & Mougin, 1986; Wang Zipan & Norman, 1993), capture of shoaling fish and krill at the sea surface (Furness & Hislop, 1981), and kleptoparasitism and piracy (Furness, 1978, 1987). Sub-Antarctic islands provide skuas with a considerable variety of potential prey, a situation that suits their opportunistic habits (Osborne, 1985; Moncorps *et al.,* In press). The diet of brown skuas has already been studied in several sub-Antarctic islands, probably because their habits of producing pellets and leaving recognizable prey remains make investigations of their diet relatively easy (Moncorps *et al.*, In press). Skuas appear to feed on the most abundant prey, such as petrels or penguins, depending on the locality. Two aspects of predation by skuas on burrowing petrels have not yet been investigated: first, it is not known whether skuas are selective in their choice of food items; second, their impact on their prey populations has never been quantified.

This study is based upon regular collection of fresh prey remains throughout the whole breeding cycle of the

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brown skua (i.e. from October to March). We investigated skua diet both qualitatively and quantitatively. This allowed us to calculate daily capture rates and to establish some comparisons between pairs, especially in terms of territory size and quality (relative abundance of prey), and breeding status and success of pairs. We investigated whether skuas were selective in their diet, tuning their choice of prey, and their timing of breeding to colony attendance of their main prey species. Finally, we tried to estimate the impact of skua predation on the burrowing petrel populations.

MATERIALS AND METHODS

Study area

The study was carried out on Mayes Island (48°28′ S, 69°57′ E), an island of 2.3 km^2 within the Morbihan gulf of the Kerguelen archipelago (Fig. 1). The islands within this sheltered gulf typically have dry soils covered with dense vegetation, providing diverse and highly suitable breeding sites for burrowing petrels. Petrels breed there in very high densities (Weimerskirch, Zotier & Jouventin, 1989), with up to 6 burrows per square metre in some areas (Mougeot, pers. obs.). The vegetation of Mayes Island has remained intact because of the absence of introduced mammals (except for the house mouse *Mus musculus*). Thirteen petrel species breed there: the blue petrel (*Halobaena caerulea*), thin-billed prion (*Pachyptila belcheri*) and common diving petrel (*Pelecanoides urinatrix*) are the most numerous. Other species are less abundant though sometimes numerous locally, and include white-headed petrel (*Pterodroma lessoni*), great-winged petrel (*Pterodroma macroptera*), Kerguelen petrel (*Pterodroma brevirostris*), grey petrel (*Procellaria cinerea*), white-chinned petrel (*Procellaria aequinoctalis*), South Georgian diving petrel (*Pelecanoides georgicus*), Wilson's storm petrel (*Oceanites oceanicus*), black-bellied storm petrel (*Fregetta tropica*) and grey-backed storm petrel (*Garrodia nereis*). All but the storm petrels are burrowing petrels. Other seabirds include the rockhopper penguin (*Eudyptes chrysocome*), breeding on the rocky coasts, lesser sheathbill (*Chionis minor*), Kerguelen shag (*Phalacrocorax albiventer*), northern giant petrel (*Macronectes halli*), Kerguelen tern (*Sterna virgatta*) and Kerguelen pintail (*Anas eatoni*).

The brown skua

Around 80 pairs of brown skua normally breed on Mayes Island (Weimerskirch *et al.*, 1989). In summer 1991, 85 breeding pairs and nearly 100 non-breeders (these were concentrated in two clubs) were censused. Additionally, skuas from nearby islands occasionally visit Mayes Is. at night to hunt (Mougeot, pers. obs.). The skua density on Mayes Island (37 breeding pairs km^{-2}, and *c.* 117 skuas km^{-2}, including the non-breeders) is thus one of the highest in the sub-Antarctic (for comparison, 100 pairs km^{-2} on Bird Is., South Georgia (Osborne, 1985), 56 pairs km^{-2} on Chatham Is. (Young, 1978) and 4–20 pairs km^{-2} on Macquarie Is. (Jones & Skira, 1979)). On Mayes Is., most skuas are currently ringed with metal and Darvic plastic colour bands, enabling individual identification at a distance. We mapped skua territories of breeding pairs (see Fig. 1) by observing agonistic interactions between neighbouring pairs, as well as from nocturnal feeding locations of individual skuas. As this method does not provide a precise estimate of size, territories were then classified in three categories according to their area. The breeding success and the breeding pattern of each pair was monitored in austral summers of 1992–93 and 1993–94 (there was no change of partners between the two breeding seasons). On Kerguelen, first returns usually occur in early October, laying was between mid-October and late November, and fledging from late January to early March. Brown skuas do not winter on Mayes Is., nor on the Kerguelen archipelago, in general, although a few individuals sometimes stay at king penguin colonies, or near the research station where they can benefit from human refuse (Mougeot, pers. obs.).

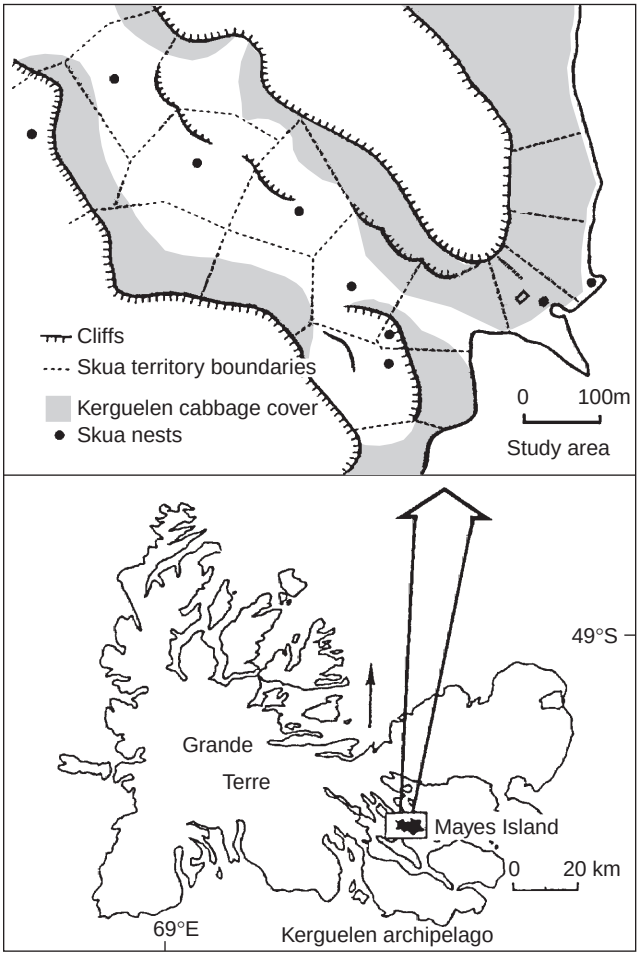

Fig. 1. Location of brown skua nests and territories on study area, Mayes Island, Kerguelen archipelago.

Collection of remains

The diet of 11 pairs (10 breeding and 1 non-breeding) of brown skuas was studied from October 1992 to April 1993. Prey remains were collected daily or every second day in the vicinity of nests. Usually, skuas carry their prey back within 10 m around the nest (this is especially true for petrels, Mougeot, pers. obs.). Less than 5% of all prey remains were found from 25 to 50 m from nests or chicks, and none farther, and we therefore confidently assume that we found virtually all prey remains for a given pair. The possibility, however, remains that some prey were caught and/or consumed outside the territory at night, and as these prey were not carried back to the nest, they were missed. In the following, we therefore deal with apparent, or observed capture rates rather than absolute capture rates. We did not collect pellets, because they are difficult to find in densely vegetated areas, are scattered, and may be regurgitated outside the territory. This may represent a possible bias in our assessment of diet, as prey remains or pellet collection can provide slightly different results (see Moncorps *et al.,* In press). Old remains were removed from all study territories during the first collection. Only fresh remains were collected, and they were removed daily from the territories. Remains generally consisted of the 2 wings connected by the sternum. Sometimes, however, isolated wings were found: in order to avoid double counts, only right wings were taken into account. Very rarely, a complete petrel corpse was found, and these were left in the territory. Species identification was on the basis of morphological features, feather colour and wing measurements.

Petrel attendance at breeding colonies

We used mist-netting in order to estimate colony attendance of the different species of petrels over the whole breeding season (e.g. James, 1985; Bretagnolle, 1990, Mougeot, pers. obs.). Two nets (12 m in length) were placed at night within the skua study area on Mayes Island. Captures began 1 hour after sunset and were performed, without tape lure, for at least 4 (but usually 6–8) hours per night. Mist-netting was performed daily from October 1992 to March 1993, thus covering the complete breeding cycle. We used the mean number of captures night^{-1} hour^{-1} for each petrel species as an index of overall attendance of the breeding colonies. This included both breeding and non-breeding birds (i.e. immatures and birds looking for burrows or partners).

Relative abundance of prey on territories of skuas

Although burrowing petrels are extremely numerous on Mayes Is., their population sizes have not been estimated accurately: several hundred thousand pairs is a likely figure. We therefore did not estimate the abundance of burrowing petrels on each skua territory, but used an indirect index, based on vegetation and soil depth. These 2 factors are known to correlate well with distribution and abundance of petrels (Strange, 1980; Croxall & Prince, 1980; Brothers 1984; Schramm, 1986; Weimerskirch *et al*., 1989; Genevois & Buffard, 1994). In our study area, 2 main types of vegetation occurred: Kerguelen cabbage (*Pringlea antiscorbutica*), providing high and dense vegetation with deep soils, where breeding blue petrels are particularly numerous; and the fell field assemblage with *Azorella* cover and thin rocky soils with sparse vegetation, favoured by thin-billed prions (although the latter also breed in *Pringlea* areas, but in lower density: Weimerskirch *et al*., 1989; Genevois & Buffard, 1994). Territories dominated by *Pringlea* were therefore dominated by blue petrels, whereas territories dominated by *Azorella* were dominated by thin-billed prions, although both species occurred in both vegetation types.

Statistical analysis was performed using Stat-ITCF and SAS statistical package (SAS, 1988). Data were first checked for normality, log-transformed if necessary, and if still non-normally distributed, non-parametric procedures were used.

RESULTS

Diet composition

A total of 2419 prey remains was collected at the 11 skua sites. Only remains of burrowing petrels were found, showing that skuas specialized in their capture, although other prey types, i.e. small items such as chicks, may have been missed because of our method. Field observations of skuas indicated a slightly more diversified diet: for instance, they were seen catching mice (mostly in April and May when these are particularly abundant), and chick predation on lesser sheathbills as well as cannibalism have also been reported once each. However, such cases were very rare. Eight petrel species were represented in skua remains (Table 1), and the blue petrel and the thin-billed prion together accounted for 92% of the diet. Blue petrel remains comprised on average 72.9% (range 59.7 to 85.8%) of all remains collected. Thin-billed prions were of secondary importance, with 19% of the remains (range 10 to 26.9%). These results indicate that brown skuas are highly specialized, as no other prey accounted for more than 7.5% of the total (Table 1). All but three of the burrowing petrels that breed on the island were found in remains: no South Georgian diving petrel, Kerguelen petrel and black-bellied storm petrel were found, but these species are the least common petrel species on Mayes Island. Although Antarctic prions do not breed on Mayes, they do so on nearby islands, and non-breeders occasionally visit Mayes in December–January during the intense courtship periods of the thin-billed prion, explaining why they were found in small numbers in remains.

Table 1. Incidence of food remains (%), collected at or near nest sites, and territory characteristics for the 11 skua sites studied on Mayes Island (October 1992–March 1993), Kerguelen

Nest number	1	2	3	4	5	6	7	8	9	10	11	All nests
Food remains collected	178	297	320	212	197	176	160	289	160	212	216	2419
Prey type (%):												
Blue petrel	61.2	83.1	80.3	63.6	65.4	59.7	82.5	75.5	60.0	85.8	84.9	72.90
Thin-billed prion	26.9	11.1	16.8	26.8	24.8	24.5	10.0	19.3	23.1	11.8	13.8	19.00
Antarctic prion	0.6	0	0.3	0	0	0	0	0	0	0	0	0.08
Common diving petrel	3.4	2.7	0.3	1.5	3.6	2.8	0	2.4	7.5	1.4	1.3	2.44
White-headed petrel	0	0.6	0	1.0	0.6	0.5	0.6	0	0	0.5	0	0.35
Great-winged petrel	0	0	0	0	0	0	0	0	0	0.5	0	0.05
Grey petrel	0.6	0	0	0	0	0	0.6	0	0.6	0	0	0.17
Grey-backed storm petrel	0	0	0	3.9	0	0	0	0	0	0	0	0.35
Unidentified	7.3	2.5	2.3	3.3	5.6	12.5	6.3	2.8	8.8	0	0	4.7
Skua territory size	1	3	3	3	2	2	3	3	1	2	3	
% of *Pringlea* cover	70	75	75	40	60	70	70	90	80	85	90	

Variations between skua territories

Territories differed significantly in the specific composition of remains, considering four classes: blue petrel, thin-billed prion, other species as a single prey category, and unidentified items ($\chi^2 = 85.9$, $d.f. = 3$, $P<0.0001$; data from Table 1). Daily (observed) capture rates were obtained for nine territories (where collections were made every one or two days): they differed significantly between skua territories (one-way ANOVA, $F_{8,116} = 6.09$, $P<0.0001$), especially for the daily capture rate of the blue petrel ($F_{8,116} = 10.35$, $P<0.0001$) and for the least predated petrels ($F_{8,116} = 2.55$, $P = 0.0135$), but there was no significant difference between territories in the daily capture rate of the thin-billed prion ($F_{8,116} = 1.44$, $P>0.05$).

The average daily capture rate of petrels by brown skuas significantly increased with territory size ($Rs = 0.67$, $P<0.05$, $n = 9$ skua sites), skuas with large territories catching more prey than those with intermediate or small territories (Fig. 2). At the species level, this was true for the blue petrel ($Rs = 0.76$, $P < 0.05$, $n = 9$) but not for the thin-billed prion ($Rs = 0.36$, $P > 0.05$, $n = 9$). For the least frequently recorded prey, mean daily capture rates decreased when territory size increased ($Rs = -0.64$, $P<0.05$, $n = 9$), which suggested that, in small territories, skuas paid more attention to such prey. However, there was no evidence that territory size affected breeding success ($Rs = -0.30$, $P>0.05$), although sample size was small ($n = 11$ pairs). Furthermore, breeding success differed between the breeding seasons of 1992–93 and 1993–94, although territories remained stable and partners unchanged.

The relative proportion of the vegetation types for the 11 skua territories are presented in Table 1. *Pringlea* cover varied from 40 to 90% (and fell field and *Azorella* accordingly from 10 to 60%). Territories were then classified into two categories, according to whether they presented more, or less, than 75% of *Pringlea* cover. Five of six skua breeding pairs with more than 75% of *Pringlea* cover on their territories had more than 70% of blue petrel in their diet, while one of the five remaining pairs had less than 70% of blue petrel (and more than 20% of thin-billed prion) in their diet (*G*-Test: $G = 8.5$, $P = 0.004$). This suggested that the overall incidence of blue petrel and thin-billed prion in the diet of pairs of skuas matched vegetation of their territory, and hence their respective abundance.

Capture rates of prey according to breeding stage and breeding success of brown skuas

Breeding pattern of skuas was studied on the basis of relative date to investigate the effect of pair breeding timing upon prey intakes. Daily petrel capture rate day^{-1} territory^{-1} significantly varied according to breeding stage (prelaying, laying, incubation, early and late chick-rearing) of brown skuas (Fig. 3, One-way ANOVA, $F_{4,35} = 8.5$, $P<0.0001$). Capture rates were highest after hatching (2.2 prey day^{-1} territory^{-1}), but decreased during chick-rearing and were lowest after

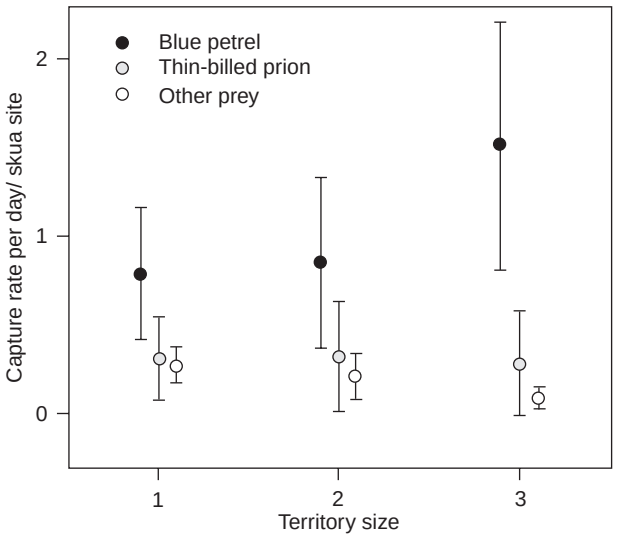

Fig. 2. Capture rates (mean ± S.D.) day^{-1} skua site^{-1} for blue petrel, thin-billed prion and other prey species according to territory size: 1 = small, 2 = intermediate and 3 = large.

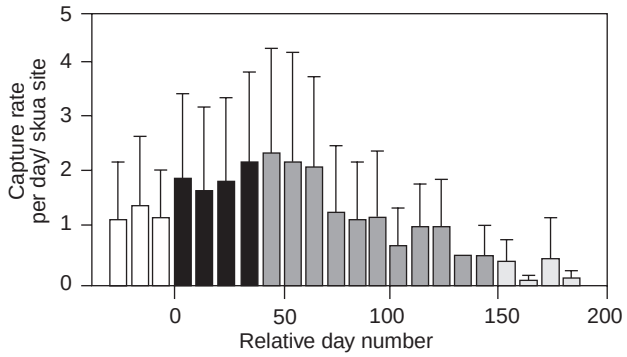

Fig. 3. Capture rate (mean ± S.D.) of petrels day^{-1} skua site^{-1} calculated for periods of 10 days according to breeding phenology of brown skuas (day 0 = laying onset, prelaying □, incubation ■, chick-rearing ▩, and fledging □).

fledging (1.0 prey day^{-1} territory^{-1}). Between-stage differences were especially marked for blue petrel intakes ($F_{4,35} = 3.64$, $P = 0.014$), thin-billed prion intakes ($F_{4,35} = 2.80$, $P = 0.04$), but not for those of other prey ($F_{4,35} = 2.33$, $P = 0.08$).

Of the nine pairs that were studied in 1992–93, eight were breeding and one was non-breeding. All breeding pairs had a clutch size of two, produced two hatchlings, but five pairs fledged two chicks while three had only one. Breeding failure was only observed during early chick-rearing. Prey capture rates were not significantly different between breeders with 1 or 2 fledglings, even when controlling for the breeding stage (two-way ANOVA: $F_{1,39} = 0.01$, $P = 0.97$ for breeding success; $F_{1,39} = 10.37$, $P = 0.003$ for breeding stage, and $F_{1,39} = 0.51$, $P = 0.48$ for the interaction). The fact that capture rates did not differ, however, may not necessarily mean that consumption rates were identical, as adults and/or chicks could sometimes eat the prey completely, or only part of it, possibly depending on availability of prey.

Laying date varied between study skua pairs: the earliest laid in mid-October and the latest in mid-November. Capture rate of all prey significantly decreased with increasing laying date (Fig. 4, $Rs = -0.92$, $P<0.001$, $n = 8$ pairs). This was especially true for intakes of blue petrel ($Rs = -0.89$, $P<0.01$), but not for intakes of thin-billed prion ($Rs = 0.01$) or of other prey ($Rs = -0.18$). Thus, early breeders brought back more prey, and especially more blue petrels, than late breeders. Prey capture by skuas was related to attendance of the main prey species at their colonies. To investigate differences in diets according to the breeding timing of skuas, we calculated for each pair and each breeding stage (prelaying, laying, incubation, early and late chick-rearing) a thin-billed prion/blue petrel ratio of captures. This ratio of capture was negatively correlated with laying date during prelaying ($Rs = -0.86$, $P<0.01$, $n = 8$ pairs), positively correlated with laying date during late chick-rearing ($Rs = 0.69$, $P = 0.05$), but did not vary between pairs during laying ($Rs = 0.59$), incubation ($Rs = 0.52$) and early chick-rearing periods ($Rs = 0.23$).

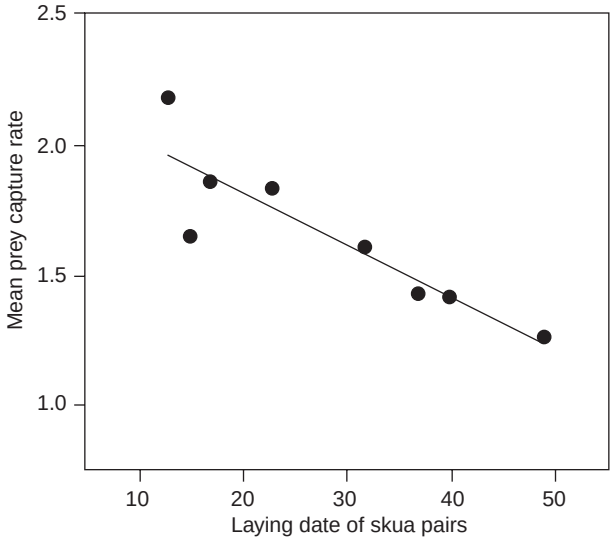

Fig. 4. Capture rate day^{-1} skua site^{-1} of blue petrel according to laying date of breeding skuas (day 0 = 1 October).

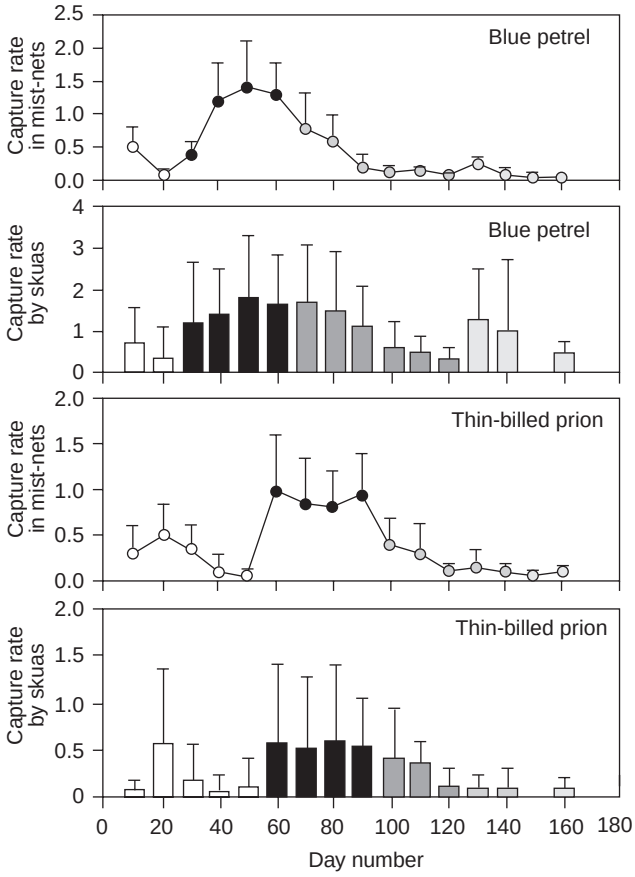

Fig. 5. Attendance rate on breeding colonies (mean captures in mist-nets hour^{-1} night^{-1}) and capture rate by brown skuas (capture day^{-1} skua site^{-1}) of blue petrel and thin-billed prion throughout their breeding cycle. Means (± S.D.) are calculated for periods of 10 days (day 0 = 1 October). Breeding phenology of petrels: prelaying □, incubation ■, chick-rearing ▩ and fledging □.

Thus, late breeding skuas caught, or at least brought back more thin-billed prion than early breeding ones at the end of chick-rearing, whereas the reverse was found during prelaying. In the early breeding skuas, hatching was synchronized with incubation stage of the blue petrel, when blue petrel availability was greatest (Fig. 5), providing abundant prey for the early stages of the rearing of skua chicks. Fledgling of early breeding skuas coincided with the fledglings of blue petrel, providing abundant prey at this period. Late breeders, in the last stages of rearing the chick, may have compensated for a lack of blue petrels in January by catching more thin-billed prions. Furthermore, the breeding timing of individual skua pairs showed some constancy between years, as laying dates of the 92–93 and 93–94 breeding seasons were positively correlated ($Rs = 0.73$, $P<0.05$, $n = 8$ pairs). However, this synchronization with the main prey, the blue petrel, did not enhance breeding success, which did not differ between early and late breeding skuas in 92–93 and 93–94 breeding seasons.

Petrel colony attendance and its incidence on skua diet

During the 169 nights of mist-netting, 5589 petrels were caught. Three species accounted for more than 90% of these captures: the blue petrel (34.5 %), the thin-billed prion (29.5 %) and the common diving petrel (27.5 %), with other petrel species totalling 8.5 %. The three former species were the main prey of brown skuas. However, relative abundance of these species, inferred from mist-netting, differed from their incidence as prey items ($\chi^2 = 35.9$, *d.f.* = 3, $P<0.0001$). The major contribution to this statistic came from the over-representation of the blue petrel (*G*-test, $G = 32.1$, $P<0.0001$) and/or the under-representation of the common diving petrel as prey items ($G = 25.7$, $P<0.0001$). The thin-billed prion showed no difference ($G = 2.5$, $P = 0.12$) and differences with respect to the other species were also minor ($G = 0.29$, $P = 0.59$). Thus, in our study area, brown skuas were selective in their prey choice.

The variations over time of predation patterns were analysed considering the two main prey species, the blue petrel and the thin-billed prion. Captures day^{-1} skua site^{-1} of blue petrel varied over time (Fig. 5), with two maximums of 1.8 blue petrel day^{-1} skua site^{-1} in the second 10 days of November, during laying period, and of 1.3 blue petrel day^{-1} skua site^{-1} in February, during the fledging period. Fledgling birds then represented 40–90% of the captures. Interestingly, the pattern of attendance of blue petrels on colonies varied similarly over time (Fig. 5). More specifically, captures day^{-1} skua site^{-1} of blue petrel were positively correlated with blue petrel attendance at colonies, as measured by mean captures hour^{-1} night^{-1} in mist-nets ($Rs = 0.32$, $P = 0.027$, $n = 47$ nights).

Intakes of thin-billed prion by skuas also varied over time, with two peaks: 0.55 thin-billed prion day^{-1} skua site^{-1} in mid-October, during prenuptial returns to colonies, and 0.4 to 0.6 bird day^{-1} skua site^{-1}, from late November to mid-January, during laying, incubation and hatching. During the fledging period, capture rates of thin-billed prion remained low (0.1 capture day^{-1} skua site^{-1}) and skuas mainly caught fledglings (40–58% of captures). Attendance of thin-billed prions on colonies (mean capture rates in mist-nets) varied in the same way over time (Fig. 5; $Rs = 0.46$, $P<0.001$, $n = 47$ nights). Thus, prey intake by skuas reflected the colony attendance patterns of the two main prey species, the blue petrel and the thin-billed prion.

DISCUSSION

High prey specificity in the diet of brown skuas

Catharacta skuas have diverse feeding techniques and diets, and these predators can use several methods to take a great variety of prey throughout their breeding range (Stonehouse, 1956; Young, 1978; Furness, 1979, 1981, 1987; Sinclair, 1980; Trivelpiece *et al.*, 1980; Green, 1986; Pietz, 1987; see also Table 2). The diets of brown skuas seem to be more diversified in sub-Antarctic islands than in Antarctica (Table 2), where breeding populations rely mainly on penguin colonies (Burton, 1968; Trivelpiece *et al.,* 1980; Cordier *et al.*, 1983), though not exclusively (see Heatwole *et al.*, 1991; Wang Zipan & Norman, 1993; Young, 1994). Differences in food remains collected in different areas suggest some degree of specialization, and this mostly seems to be related to local availability of resources (Moors, 1980; Schramm, 1983; Osborne, 1985; Wang Zipan & Norman, 1993). This specialization within localities is especially well marked for petrels (Table 2): in most places, a single species of petrel accounts for more than half of the prey found in remains or pellets. On Mayes Island, there is a great range of potential avian prey species, but brown skuas are highly dependent on burrowing petrels and feed mainly on two species, the blue petrel and the thin-billed prion. Our results resemble those obtained on Prince Edward Island (Adams, 1982; Schramm, 1983), where the blue petrel is also the main prey.

Incidence on diet of local abundance of prey

In most of the studies so far conducted, the incidence of petrel prey in diets of brown skuas reflected their local abundance, and distribution of breeding skuas may depend on resource distribution (Jones & Skira, 1979; Stahl & Mougin, 1986; Wang Zipan & Norman, 1993). In our study area, the blue petrel and thin-billed prion show distinct nest-site preferences (Weimerskirch *et al.,* 1989; Genevois & Buffard, 1994). Representation of these species in diets of brown skuas can be taken to reflect territory quality, which can also be inferred from vegetation. However, territory quality should be considered with caution, as brown skuas can sometimes feed

Table 2. Review of diets of *Catharacta* skuas in localities where they capture burrowing petrels

Subspecies - Localities	Petrels (%)	Main prey species (1)	Method	Sources (2)
Brown skua (*Catharacta skua lönnbergi*)				
- Chatham Is.	90	BBP, WFSP, CDP	P + R	Young, 1978
- Antipodes Is.	> 90	WHP (73%)	R	Moors, 1980
- Bollons & Archway Is.	> 95	SPP (92%), GP	R	Moors, 1980
- Macquarie Is.	> 90	AP (50%), WHP	R	Jones, 1980
- Possession Is. (Crozets)	12.5	SaP, CDP	P + R	Stahl & Mougin, 1986
- East Is. (Crozets)	72	SaP (55%), CDP	P + R	Stahl & Mougin, 1986
- Prince Edward Is.	> 80	BP (65%), KP	R	Adams, 1982
- Mayes Is. (Kerguelen)	> 95	BP (73%), TBP	R	This study
Tristan skua (*Catharacta skua hamiltoni*)				
- Inaccessible Is. (Tristan da Cunha)	> 90	BBP, WBSP, WFSP	P + R	Fraser ,1984
- Gough Is. (Tristan da Cunha)	> 95	BBP, SPP	R	Fraser, 1984
South polar skua (*Catharacta skua maccormicki*)				
- P. Elizabeth Land:	72	SnP (66%), WSP	P + R	Wang Zipan & Norman,1993
- near Davis:	70	WSP, AF, SnP	P	Green, 1986
- Hope Is.:	> 40	AF (24%), SnP	P	Norman & Ward, 1990
Great skua (*Catharacta skua skua*)				
- Foula (Shetland):	5	BSP (5%)	P	Furness, 1987

(1) Main petrel prey species: WFSP: white-faced storm petrel; WBSP: white-bellied storm petrel; WSP: Wilson storm petrel; BSP: British storm petrel; CDP: common diving petrel; WHP: white-headed petrel; SPP: soft-plumaged petrel; KP: Kerguelen petrel; GP: grey petrel; AP: Antarctic prion; BBP: broad-billed prion; SaP: Salvin s' prion; TBP: thin-billed prion; BP: blue petrel; AF: Antarctic fulmar; SnP: snow petrel.
(2) Method used for diet analysis: P = pellets; R = remains; P + R = pellets and remains.

both on and off the territory (Young, 1994). On Mayes Island, brown skuas exhibited vigorous territorial defence, territories were very small and presumably easily patrolled, and feeding outside the territory probably seldom, if ever, occurred. Most of the intruders were skuas from nearby islands, probably non-breeding birds, that came at night to hunt on colonies. Indirect surveys of burrowing petrels based upon prey remains have been made on Marion Island (Adams, 1982; Schramm, 1983) and Macquarie Island (using remains left by skuas and by feral cats, see Jones, 1980) in order to investigate the specific distribution and the relative frequencies of petrel species. This method must be restricted to species vulnerable to skua predation and may be subject to bias if individual skuas show prey specialization within localized areas or territories (Jones, 1980; Adams, 1982). In this study, we have shown that skuas can be locally selective in their prey intakes. The main prey, the blue petrel, was preferred to all other species. This was especially marked in the case of brown skuas holding large territories. Incidence in diets of minor prey species, such as diving petrels, did not reflect local abundance. Evidence from studies involving both pellets and prey remains indicates that these methods underestimate the incidence of small prey, presumably because small birds may often be swallowed whole by skuas (Fraser, 1984; Stahl & Mougin, 1986; Moncorps *et al.,* In press). On Mayes island, common diving petrels are locally abundant in colonies, particularly in Kerguelen cabbage areas (Weimerskirch *et al*., 1989) and seemed to be avoided by skuas. Common diving petrel could be an unprofitable prey for skuas on Mayes Island. Determining the search effort of brown skuas could improve techniques of indirect survey (Adams, 1982), but this may depend on many different factors.

Variations of capture rates over time according to colony attendance of prey species

There have been very few studies on the nature of predation on petrels. The incidence of the broad-billed prion in the diet of Tristan skuas decreased in December–January with a corresponding increase in common diving petrel (Fraser, 1984). Stahl & Mougin (1986) studied the diet of the brown skua on East Island from October to January and found little change in the representation of petrels in diets (98.5% in October to 91.8% in January), mainly due to a decrease of common diving petrel. On Possession Island, where petrels represented only 7.9% of prey, their incidence in diets changed very little from October to February. On Princess Elizabeth Land, Antarctica, intakes of snow petrel by South polar skua varied over time according to the attendance of prey species on their breeding grounds (Wang Zipan & Norman, 1993). In our study area, the capture rates of the two main prey species were

related to their respective attendance on colonies, measured by capture rates in mist-nets. For blue petrel and thin-billed prion, we found maximum rates of capture, by skuas and in mist-nets, to be during laying and hatching, which coincided with periods of intense courtship performed by non-breeding birds (pers. obs.). Attendance on colonies was then increased because cohorts of immatures and non-breeding birds came to colonies at this time. Captures by skuas also increased during prenuptial returns to colonies, when petrels reoccupy burrows and engage in courtship behaviour (in late September for blue petrel and mid-October for thin-billed prion). Field observations have suggested that skuas were more likely to catch petrels while they were in the open rather than in burrows (Young, 1978; Fraser, 1984; Furness, 1987, pers. obs.). Breeding petrels that possess a burrow generally land at its entrance and rapidly disappear underground, whereas non-breeders looking for a burrow and a mate exhibit conspicuous behaviour (vocal displays) and have to stay in the open where they are more vulnerable to skuas (Furness, 1987; Young *et al.*, 1988, pers. obs.). On Gough Island, immature, non-breeding broad-billed prions, that have a narrower bill width than breeding birds, apparently represented a large proportion of the birds killed by skuas (see Furness, 1987). This coincidence of periods of maximum capture with periods of attendance of non-breeding birds and intense vocal displays on colonies suggests that most of the blue petrels and thin-billed prions killed by skuas then were non-breeders.

Variations of capture rates of petrels according to breeding stage and success of skuas

Failures in breeding of study pairs, that were due to chick mortality, were apparently not related to capture rate of brown skuas, at least as estimated through prey remains. Conversely, in the great skua, egg loss increases when food availability is low and breeding density high (Furness, 1984). In the South polar skua, the loss of a chick in two-chick broods can be related to food availability (Procter, 1975), but chicks may be lost for several reasons such as exposure and predation (Young, 1963; Spellerberg, 1971) and also aggressive behaviour, that predispose the second chick to mortality from other factors. On Princess Elizabeth land, Antarctica, Wang Zipan & Norman (1993) found that capture rates of snow petrels by South polar skuas reflected not only the breeding status of skuas, but also the stage, the success and the demands of breeding itself. Three possible reasons may account for this discrepancy of results: territories were not defined precisely enough, sample size was too small, or capture rate does not accurately represent consumption rate.

On Mayes Island, capture rates of prey differed according to breeding stage of brown skuas, and were greatest after hatching. Then, prey intakes decreased during chick-rearing. In sub-Antarctic localities, the breeding of the predominant prey species may have influenced the timing of the skua breeding cycle (Osborne, 1985; Young, 1994). Skuas would be expected to adjust their needs to local abundance in synchrony with their main prey, even if their habits of storing food in 'larders' may allow a certain plasticity (see Stahl & Mougin, 1986; Furness, 1987). On Mayes Island, laying dates of skuas show some variation (nearly a month in this study), and we found significant differences in capture rates of blue petrel between early and late breeders for some periods. Early breeders seemed to be well synchronized with the availability of blue petrels, whereas late breeders had to compensate by catching thin-billed prions at certain times.

Impact of brown skuas on the population of burrowing petrels

The real impact of skuas on burrowing petrel populations is still poorly documented. Few studies gave daily rates of capture of petrels, and none over long periods as in our study. The great skua on Foula (Shetlands), may take an average of 5% of the British storm petrel population breeding on this island each year, estimated as 9000 birds (see Furness, 1987). On Chatham Island, Young (1978) made daily collections of remains in December and January and found that some skuas caught 2–3.3 broad-billed prions day^{-1} skua $site^{-1}$ (4 sites), with a highest average of 4.8 prions day^{-1} skua $site^{-1}$, and for three other sites, capture rates were 0.7–1.8 prey day^{-1} skua $site^{-1}$. These results are similar to ours, brown skuas catching, for the same period, 2–2.5 petrel day^{-1} skua $site^{-1}$, with a maximum average of 3.8, and they also show great variations between pairs. Mean capture rates of petrels per skua site, calculated for the whole course of the study and for the 11 sites, were 1.68 ± 1.34 prey per day (1.2 ± 1.24 blue petrel per day and 0.31 ± 0.57 thin-billed prion per day, $n = 662$ collections). On Mayes Island, the population of brown skua was estimated at 85 breeding pairs and 100 non-breeding skuas. If our study area is representative of the whole island, we can then estimate that, from mid-September to mid-May, more than 55,000 petrels were caught on this 2.3 km island, of which 40,000 were blue petrels. Densities of burrowing petrels are very difficult to assess on Mayes Island. In Kerguelen Cabbage areas, burrow densities can reach six burrows per square metre (pers. obs.). Density of blue petrels was estimated as 40.8 ± 3.1 burrows per 25 m^2 (i.e. 1.63 burrow per m^2), in favourable areas (Chaurand, 1992). Overall, the petrel breeding population is thought to be in the order of several hundred thousand pairs on Mayes Island. This would mean that *c.* 5–10% of the petrels there would be taken by the skuas, although it should be noted that, as suggested above, most of the predation is on non-breeders. Similar figures were found on Foula (Furness, 1987) and on Daikoku Island where slaty-backed gulls took *c.* 13% of the adult Leach's storm petrel population (Watanuki, 1986).

Procellariiformes are a long-lived species characterized by delayed sexual maturity, low fecundity and high adult survival (Warham, 1990). We therefore suggest that this kind of level of predation exerted by skuas should be considered as a strong selective pressure for petrels.

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