

ASPECTS OF THE BREEDING BIOLOGY AND FEEDING BEHAVIOUR OF THE BROWN SKUA *CATHARACTA LONNBERGI* ON BIRD ISLAND, SOUTH GEORGIA

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ABSTRACT. The breeding biology and feeding behaviour of the brown skua (*Catharacta lonnbergi*) was studied at Bird Island, South Georgia. Eggs were laid over a six-week period, with a mean laying date of 26 November. The incubation period was 29 days for both first- and second-laid eggs. First-hatched chicks were heavier than second-hatched chicks throughout the growth period and single chicks were similar to first-hatched chicks. Overall survival from eggs laid to chicks fledged was 71% (egg survival 82%, chick survival 87%). Within the population local differences exist in the timing of the breeding cycle and these might relate to variations in local prey availability.

Skuas were seen to use a variety of techniques to take a wide range of prey species. From an analysis of midden remains, dove prions, penguins (especially macaroni penguins) and common diving petrels were the most important prey species overall, but significant local variations existed, especially in the importance of seal-derived material.

INTRODUCTION

The brown or sub-Antarctic skua (*Catharacta lonnbergi*) has a wide breeding range encompassing much of the Southern Ocean from the southern Antarctic Peninsula (68° S) to the Chatham Islands east of New Zealand (44° S) (Watson and others, 1971). The species is migratory, spending only the summer months in the Southern Ocean.

A number of studies of the brown skua have been carried out in the sub-Antarctic and Antarctic regions (e.g. Stonehouse, 1956; Burton, 1968; Young, 1978; Williams, 1980) and these suggest some differences in the duration of the egg-laying period, the timing of the breeding cycle and breeding success between different populations. There are also differences in feeding behaviour, usually associated with variations in prey availability and distribution (e.g. Moors, 1980). Thus, in some areas, only one prey species is readily available (e.g. an isolated penguin colony), while in other areas there may be several species of penguin and a variety of petrels.

On Bird Island, South Georgia (54° 00' S, 34° 02' W), there is a diverse array of potential prey species each with rather different spatial and temporal availability, and the present study was undertaken to assess whether this might promote similar variation in breeding timetable and feeding ecology within a single population.

METHODS

Skuas breed throughout Bird Island though the present study was concentrated within parts of North Valley, Top Meadows, Bottom Meadows, Stejneger Peak and Goldcrest Point (Fig. 1), an area of c. 80 ha, about one-sixth of the island's surface area. These localities cover a diverse range of habitats, from open scree to deep tussock grass (*Poa flabellata*) and include, or are closely adjacent to, colonies of most of the main prey species taken by skuas.

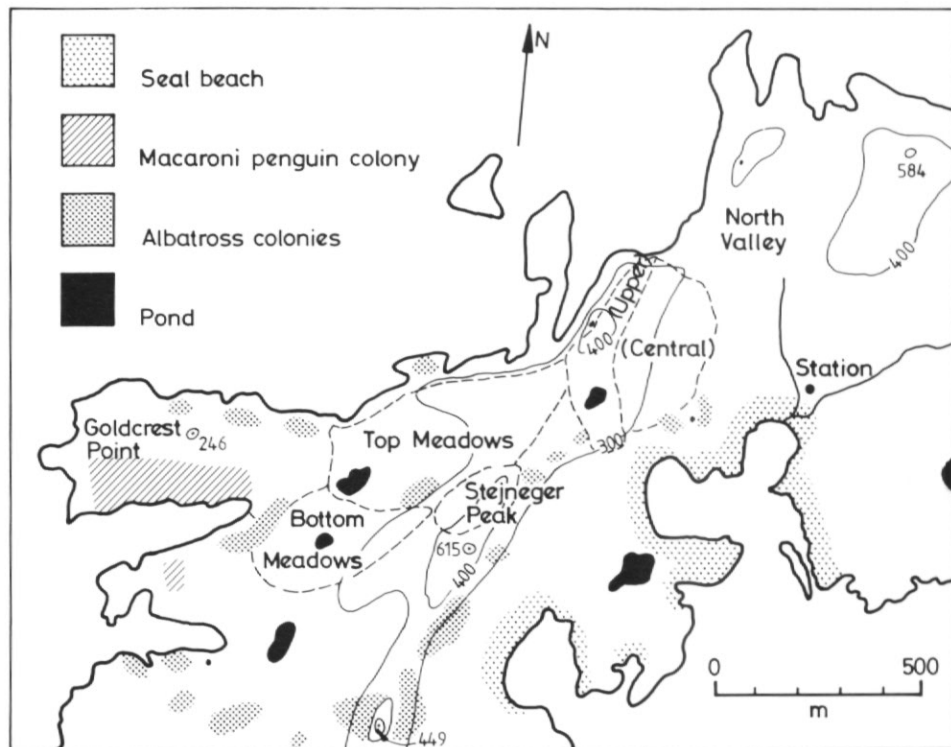


Fig. 1. Map showing the location of the different parts of the study area and the main seal, albatross and penguin colonies used by the skuas.

The breeding population of skuas on Bird Island has increased steadily during the last 25 years. Counts in 1958/9, 1976/7 and 1980/1 show 173, 300 and 375 nests respectively (W. L. N. Tickell, unpubl.; D. F. Parmelee, unpubl.; Hunter, 1981). The present study area contained 31 nests in 1958/9 and 42 nests in 1976/7 (each about 15% of the total count) and 81 nests in 1983/4, suggesting that the breeding population of the whole island might be approaching 500 pairs.

Breeding behaviour

Territories were checked daily from late October and dates of egg laying were recorded for 71 nests. The first egg laid in each nest was marked for identification at hatching or in the event of egg loss. Nests were checked regularly throughout the incubation period to detect egg loss, and daily checks were resumed just prior to the estimated hatch date for each nest. After hatching, most territories were visited periodically to assess chick mortality and fledging dates.

Chick growth

Chicks on 15 territories were weighed daily (using a bird bag or net and a Pesola spring balance) and their wing length (maximum chord) was measured with a stopped wing rule twice a week. Skua chicks are precocious (leaving the nest site within a few

days of hatching) and cryptic; their tendency to hide in deep tussock grass meant that occasionally they could not be found.

Of the 24 chicks weighed, 6 were single chicks and 18 were in broods of two chicks (hereafter referred to as 'twins'). Of the single chicks, 5 were the result of only one egg being laid in the nest or one egg failing prior to hatching. The sixth was a second-hatched chick whose older sibling died when two days old. Growth curves were obtained for all 6 single chicks. Of the twins, 13 survived to fledging and 14 reasonably complete growth curves were obtained including 7 'A' (1st-hatched) chicks and 7 'B' (2nd-hatched) chicks.

Midden collections

Most skua territories contain middens where the indigestible components of prey are regurgitated or otherwise deposited. The material on these middens is a useful guide to the prey taken by the birds on each territory. The contents of middens were collected from 38 territories during the 1983/4 breeding season.

Midden collections were neither regular nor carried out evenly across the study area and most were made before the end of December.

General observations

Between two and five hours per day were spent in the study area and any feeding behaviours seen were noted.

RESULTS

Breeding behaviour

The first skua to return after the winter arrived on 7 September and pairs were holding territories in the study area by 19 September. Several flights were observed both on territorial boundaries and within territories during October and November. Courtship feeding was seen on several occasions between members of a territory-holding pair. In the case of the pair whose territory was beside the station buildings, it was always the male who fed the female. (The female was larger and paler than the male and easily identified. The sexes were originally distinguished when the pair was observed copulating.)

One territory in the study area was occupied by three adults. The sex of each bird was not certain, but the two eggs in the nest were less similar than those of any other pair of eggs seen in the 1983/4 season. As Bonner (1964) points out, the colour, spot size and spot distribution of eggs from any one female are broadly similar, which suggests that in this case the eggs came from two different females and that the trio may therefore have consisted of one male and two females.

Copulation was observed on 18 occasions between 7 November and 5 December and for 13 of these copulations the subsequent laying date was recorded, giving a copulation-to-laying period ranging from two to 23 days (mean 11.2 ± 6.0 (SD) days). On two territories the adults were observed copulating on at least two separate occasions prior to laying and the pair nearest the base copulated on numerous occasions before the eggs were laid.

Egg laying

The first eggs were found on 4 November on Johnson Top, although they could have been laid 1-2 days earlier. In the study area, laying dates were obtained for 71

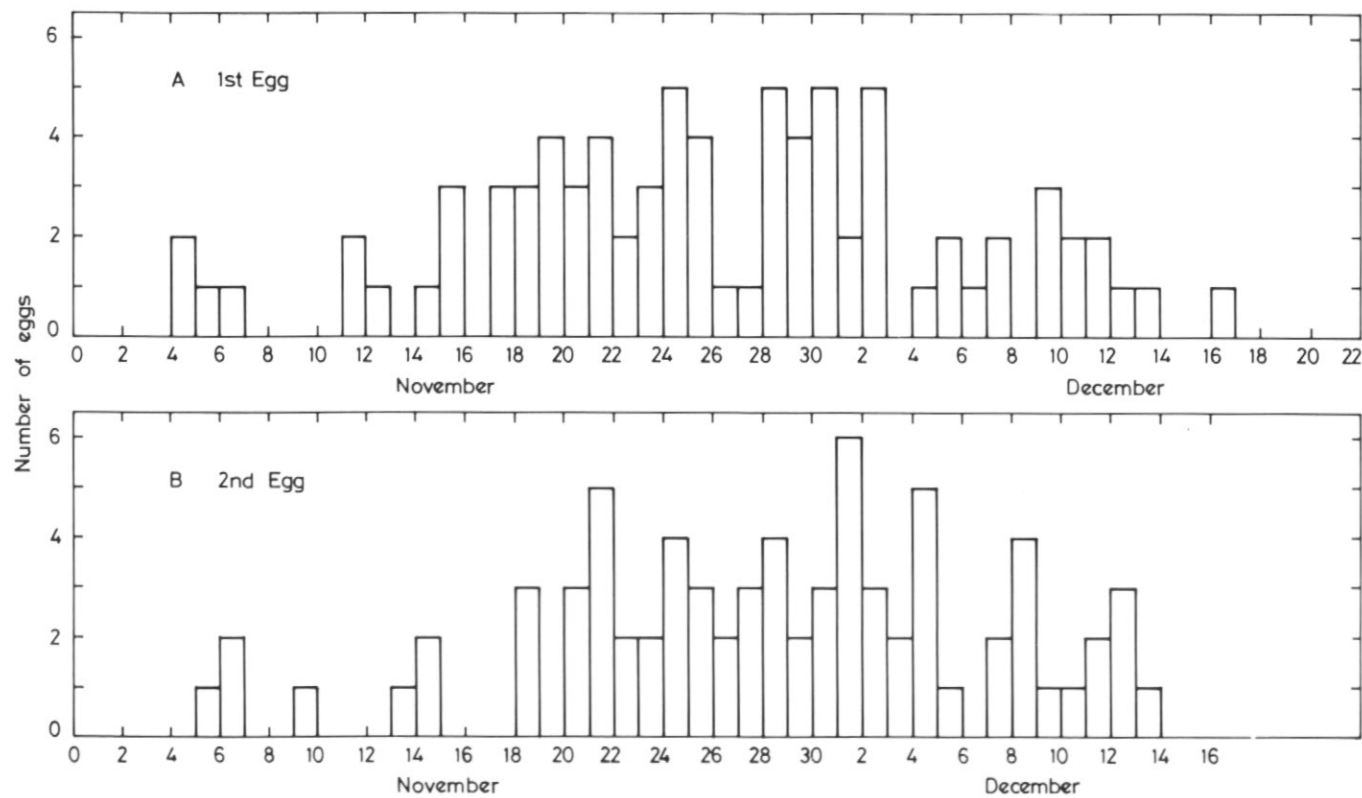


Fig. 2. Laying dates of 'A' and 'B' eggs.

'A' eggs, the first being laid on 6 November and the last on 13 December, a 38-day interval. The mean laying date for 'A' eggs was 26 November \pm 8.0 days and for 'B' eggs it was 28 November \pm 7.5 days (range 9 November to 12 December, $n = 63$). These ranges are minimum values, because a number of very early and very late eggs were missed. However, the hatching dates of such eggs were obtained, and by subtracting 29 days (the mean incubation period, see below) from the hatch date a laying date can be calculated. If these eggs are now included, the range between first and last eggs is extended to 42 days for 'A' eggs and 39 days for 'B' eggs though the mean laying date remains the same in both cases (Fig. 2).

Of the 71 nests for which laying date is known, 60 (84.6%) contained two eggs and seven (9.9%) one egg. Four nests had three eggs laid in them, though in all cases this was due to re-laying after the first egg had been lost. The timing of egg laying (and therefore of the whole breeding cycle) differs between some of the sub-areas of the study (Table I). Laying dates differed significantly between territories on Goldcrest Point and Stejneger Peak ($F = 7.812$, $P < 0.05$), Goldcrest Point and upper North Valley ($F = 13.459$, $P < 0.05$) and between Top Meadows and upper North Valley ($F = 8.366$, $P < 0.05$).

Table I. Egg laying dates in various parts of the study area on Bird Island.

Area	Laying date		
	Mean	SD	Range
Goldcrest Point	15 November	± 6 days	5 November–22 December
Top Meadows	23 November	± 11 days	4 November–13 December
Bottom Meadows	26 November	± 7 days	6 November–7 December
Stejneger Peak	26 November	± 10 days	21 November–16 December
North Valley (Central)	30 November	± 6 days	18 November–4 December
North Valley (Upper)	1 December	± 7 days	17 November–10 December

Incubation period and hatching dates

The duration of incubation was remarkably consistent. For the 'A' egg the mean incubation period was 29.5 ± 0.8 days ($n = 54$, range 28–31 days) and for 'B' eggs the mean was 29.2 ± 0.9 days ($n = 51$, range 28–31 days). The second egg showed a slightly shorter incubation period, but this difference was not significant ($t = 0.015$, $n = 103$, $P > 0.05$). The mean hatching date was 25 December for 'A' eggs and 27 December for 'B' eggs.

Fledging period and chick departure

Accurate fledging dates were obtained for 12 chicks, whose mean fledging period was 54.8 ± 4.0 days (range 50–63 days). Approximate fledging dates (to within two or three days) were obtained for a further 13 chicks whose nests were less regularly visited. The mean fledging period of the whole sample of 25 chicks was 57.6 ± 4.9 days (range 50–66 days).

Only five departure dates (i.e. when the chick finally left the territory) were recorded. These were among the very early leavers and are possibly atypical. Their mean hatch-to-departure time was 56.4 ± 4.0 days (range 53–63 days).

Table II. Weight of 'A', 'B' and single chicks at different stages during growth period.

	Weight (g)		
	A	B	Single
Day 5			
<i>n</i>	7	7	4
Mean	148	130	147
SD	12	18	15
Day 10			
<i>n</i>	7	7	6
Mean	331	286	323
SD	18	39	31
Day 20			
<i>n</i>	7	7	6
Mean	851	789	823
SD	55	58	50
Day 30			
<i>n</i>	6	7	6
Mean	1313	1146	1305
SD	75	105	127
Day 40			
<i>n</i>	4	5	4
Mean	1585	1420	1473
SD	93	116	151

Chick growth

Weights of 'A', 'B' and single chicks were compared at various ages after hatching (Table II). At 10 and 30 days 'A' chicks are significantly heavier than 'B' chicks and at 30 days single chicks are significantly heavier than 'B' chicks. Otherwise there was no significant difference between the three classes of chick although throughout the growth period the mean weights of 'A' chicks were consistently greater than those of 'B' chicks (Fig. 3). Mean weights of single chicks (not shown on diagram) were greater than those of 'B' chicks but very similar to those of 'A' chicks.

Wing growth showed slight differences between the three classes of chick (Fig. 4), but there was no significant difference between the regression coefficients of the straight-line portion of the three curves, i.e. between 15 and 45 days ('A' × 'B', $F_s = 0.036$, N.S.; 'A' × singles, $F_s = 0.037$, N.S.; 'B' × singles, $F_s = 0.011$, N.S.).

Breeding success

Of 139 eggs checked from laying to hatching, 114 (82.0%) survived to hatching including 71.4% and 86.7% of those in one- and two-egg clutches respectively (Table III). In 2-egg clutches the 'A' egg showed slightly but not significantly higher survival (88.3%) than the 'B' egg (85.0%).

Of 77 chicks that were followed from hatching to fledging, 67 (87%) survived. Of the 11 single chicks in this sample (either the result of a single egg being laid or the failure of one egg of a pair), nine (82%) were successful and 58 out of 66 (88%) twins survived (Table IV). Surprisingly, 'B' chicks showed a slightly higher survival rate than 'A' chicks (94% vs 82%), though this difference was not significant ($\chi^2 = 2.28$, $df = 3$, $P = 0.5$). The overall breeding success, from eggs laid to chicks fledged, was thus 71%.

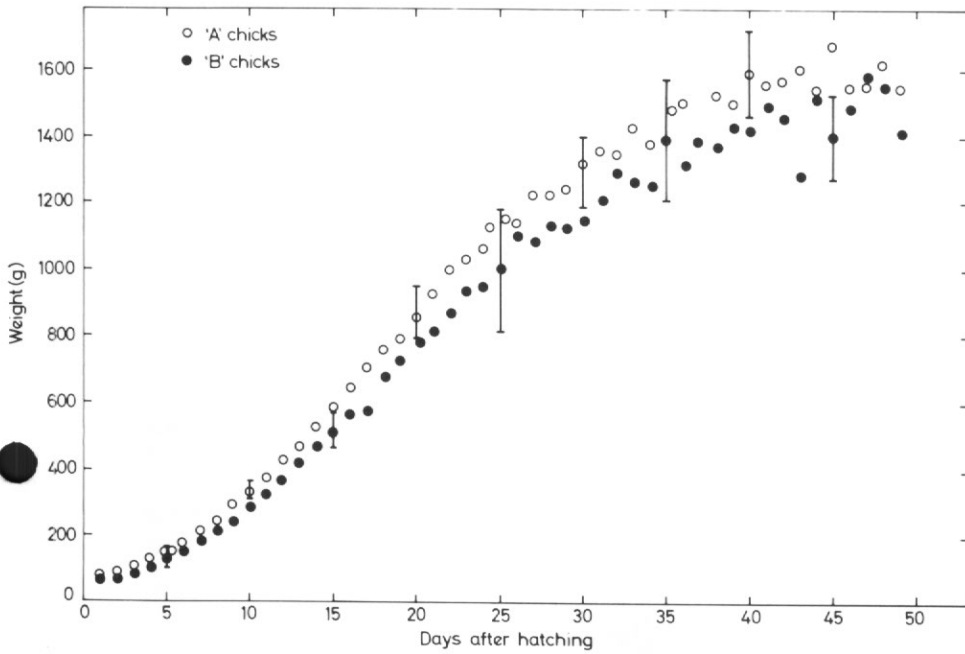


Fig. 3. Mean weights of 'A' and 'B' chicks at daily intervals from hatching to fledging. Vertical bars show SD and range at 10-day intervals.

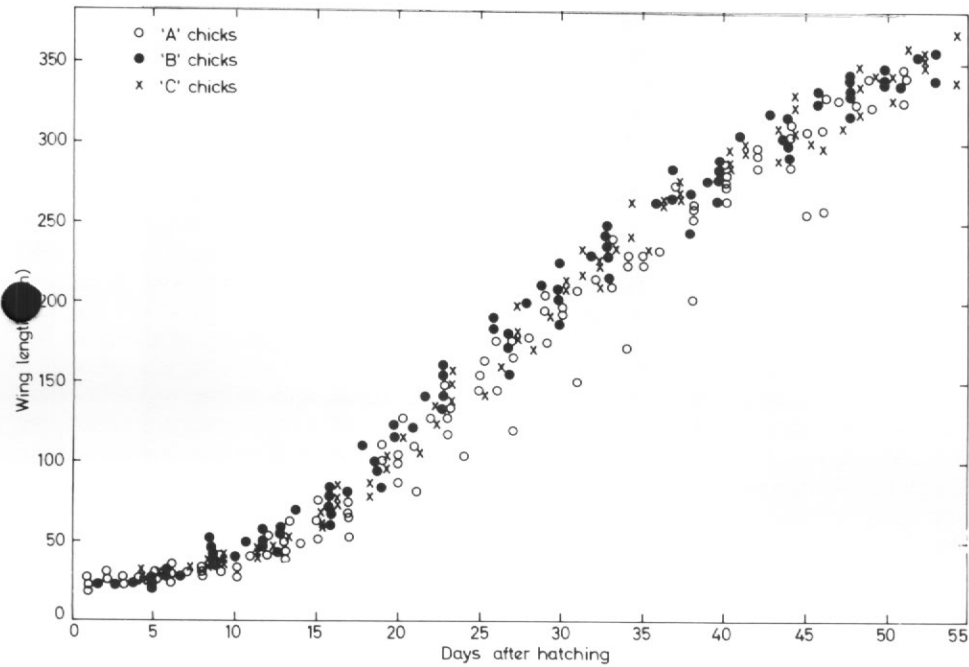


Fig. 4. Wing length of 'A', 'B' and single chicks from hatching to fledging.

Table III. Survival of skua eggs on Bird Island in the 1983/4 summer.

Eggs in clutch	Eggs laid	Eggs hatched	Survival to hatching (%)
1	7	5	71.4
2	120	104	86.7
3	12	5	41.7
Overall	139	114	82.0
'A' egg*	60	53	88.3
'B' egg*	60	51	85.0

* Data for 'A' and 'B' eggs refer to 2-egg clutches only.

Table IV. Survival of skua chicks on Bird Island in the 1983/4 summer.

Chicks hatched per nest	Total chicks hatched	Total chicks fledged	Survival from hatching to fledging (%)
1	11	9	81.8
2	66	58	87.9
Overall	77	67	87.0
'A' chick*	31	25	80.6
'B' chick*	31	29	93.5

* Data for 'A' and 'B' chicks refer to nests in which two chicks hatched.

Food and feeding

General observations

Skuas were seen taking a wide range of prey items, which included, in one form or another, most of the other birds and seals that breed on the island during the summer months. The following observations give some indication of the range of feeding techniques employed by skuas to exploit the diverse array of prey available. Common diving petrels (*Pelecanoides urinatrix*) and dove prions (*Pachyptila desolata*) suffer heavily from skua predation, and even the much larger white-chinned petrels (*Procellaria aequinoctialis*) are occasionally taken. They were either chased (and grounded) while in flight, caught while on the ground at night or dug out of their burrows while incubating. They were normally plucked before being either ingested whole by a single skua or torn apart by a breeding pair. When the skua chicks are very young (up to 10 days old), prion carcasses are brought to the nest site and the soft parts fed in small pieces to the chicks. Skuas also killed chicks of many of the larger surface-breeding species, including grey-headed albatross (*Diomedea chrysostoma*), black-browed albatross (*D. melanophris*), northern and southern giant petrels (*Macronectes halli* and *M. giganteus*), and macaroni and gentoo penguins (*Eudyptes chrysolophus* and *Pygoscelis papua*). Albatross colonies normally attract a resident pair of skuas, whereas penguin colonies are visited by large numbers of non-breeders as well as by breeding birds from nearby territories. Other species occasionally taken by skuas at Bird Island include Wilson's storm petrel (*Oceanites oceanicus*), black-bellied storm petrel (*Fregetta tropica*), South Georgia pipit (*Anthus antarcticus*) (Hunter, 1980) and South Georgia pintail (*Anas georgica*).

Eggs constitute an important part of the skua's diet and I found eggs of mollymawk albatrosses, macaroni penguins, white-chinned petrels and dove prions on skua middens.

Skuas are very efficient scavengers and the beaches surrounding Bird Island provide a rich foraging ground, especially during the Antarctic fur seal (*Arctocephalus gazella*) breeding season, when there is a plentiful supply of placentae during the pupping period and of pup carcasses for a while afterwards. Skuas also scavenge at carcasses of adult fur seals but are subordinate to giant petrels in terms of access to such prey.

Kleptoparasitism was observed frequently and involved a number of victims. Southern black-backed gulls (*Larus dominicanus*) were often chased by skuas and forced to regurgitate food items. Skuas were also seen harassing grey-headed albatrosses while the adults were in the act of feeding chicks. In these cases, the adult albatross would spill fish or squid on to the ground before flying off, thereby providing a meal for the skua. One particularly interesting case of kleptoparasitism was observed when a skua harassed a southern giant petrel chick. The chick regurgitated at the skua who immediately ate the vomit and fed it to its own chicks 10 minutes later. The giant petrel's nest was within the skua territory and skuas were seen on other occasions killing much larger giant petrel chicks. In this case, however, rather than killing and eating the giant petrel chick itself, the skua might have learnt that there was more to be gained by periodically making the chick regurgitate part of a recent meal.

Midden samples

Most midden samples contained a variety of remains including most locally available prey species. The only common species missing from the middens in the study area was gentoo penguin (eggs and chicks) though the 'penguin pellet' fraction might have contained such remains. The most important species were dove prions (remains in 97.4% of middens), penguins (feather pellets in 94.7% of middens), common diving petrels (in 60.5% of middens) and macaroni penguins (eggs in 52.6% of middens).

By combining all collections within each part of the study area a mean frequency of occurrence of each prey type per midden (total number of each prey type collected from area divided by the number of middens in area) can be calculated (Table V).

Dove prions occurred more frequently on middens in Top Meadows, Bottom Meadows and Stejneger Peak than in other areas, while diving petrels occurred more on Goldcrest Point and Top Meadows middens than elsewhere. The Goldcrest Point middens contained fewer penguin pellets than other middens, though they contained more macaroni penguin chicks and eggs. Seal remains (pellets, bones and skin fragments) were all more frequent on the North Valley (Upper) and North Valley (Central) territories than in other areas. Pairs on Stejneger Peak also exploit this resource but to a lesser extent.

DISCUSSION

Timing of breeding

Young (1977) suggested that the more southerly skua populations breed later than those further north. This study confirms that skua arrival and egg laying on Bird Island is, as expected, earlier than at Signy Island and later than at more northerly islands such as Chatham Island and Marion Island (Table VI).

The laying period of six weeks is similar to that of the northern populations but is longer than that recorded by Burton (1968) at Signy Island, where it lasted only three weeks. It is possible that at Signy the later and shorter summer prevents skuas from breeding earlier and limits the period in which they can breed successfully.

The time between arrival and egg laying varies between different study sites. On Bird Island and Marion Island skuas arrive several weeks before egg laying starts, whereas at Signy they breed relatively soon after arrival. There is no obvious explanation for these differences.

Table V. The total number and the mean frequency per midden of each type of prey collected on skua middens during the 1983/4 summer in different parts of the

study area.	Goldcrest Point	Top Meadows	Bottom Meadows	Stejneger Peak	North Valley (Upper)	North Valley (Central)	Goldcrest Point	Top Meadows	Bottom Meadows	Stejneger Peak	North Valley (Upper)	North Valley (Central)	Overall items/midden
<i>No. of middens</i>	7	15	7	3	4	2	7	15	7	3	4	2	38
<i>Species</i>	<i>Total items</i>						<i>Items per midden</i>						
Blue petrel	1	2	1	2	1	0	0.1	0.1	0.1	0.7	0.3	0	0.2
Dove prion	18	189	63	35	14	7	2.6	12.6	9.0	11.7	3.5	3.5	8.6
Common diving petrel	21	70	5	2	2	0	3.0	4.7	0.7	0.7	0.5	0	2.6
Wilson's storm petrel	0	1	0	1	2	0	0	0.1	0	0.3	0.5	0	0.1
Black-bellied storm petrel	0	4	0	0	0	0	0	0.3	0	0	0	0	0.1
Albatross chick	0	2	0	0	0	0	0	0.1	0	0	0	0	0.1
Penguin feather pellet	31	227	107	79	79	9	4.4	15.1	15.3	26.3	19.8	4.5	14.0
Macaroni penguin egg	71	50	19	0	7	4	10.1	3.3	2.7	0	1.8	2.0	4.0
Macaroni penguin chick	7	1	0	0	0	0	1.0	0.1	0	0	0	0	0.2
Fur seal pellet	0	9	0	4	25	19	0	0.6	0	1.3	8.3	9.5	1.5
Fur seal bone	1	3	5	3	70	5	0.1	0.2	0.7	1.0	17.5	2.5	2.3
Fur seal skin	0	0	0	0	2	0	0	0	0	0	0.5	0	0.1

Table VI. The timing of the brown skua breeding cycle at different sites.

Location	Latitude	First arrivals	Laying period	Source
Chatham Islands	44° 22' S	—	15 Sept.–25 Oct.	Young (1978)
Îles Crozet	46° 25' S	6 August	29 Oct.–16 Nov.	Barré (1976)
Marion Island	46° 54' S	mid August	23 Oct.–19 Nov.	Williams (1980)
Bird Island	54° 00' S	7 September	4 Nov.–13 Dec.	This study
South Georgia	54° 04' S	First week Sept.	{ 31 Oct.–15 Nov. (1953/4) 14 Nov.–29 Nov. (1954/5) }	Stonehouse (1956)
Signy Island	60° 43' S	Second week Oct.	21 Nov.–20 Dec.	Burton (1968)

There are two possible explanations for the observed differences in timing of laying dates between areas on Bird Island. Firstly, laying date may be related to the altitude, since snow is present on higher ground until later in the season and may prevent nest-building activities. Thus skuas on Goldcrest Point, the lowest part of the study area, would be expected to lay earlier than those on the Meadows and Stejneger Peak and those in North Valley would be latest to lay, as was the case. However, the 1983 winter was relatively mild and there was very little snow in any part of the study area by the end of October, which means that the usual constraints to early breeding in the high areas were not present in the 1983/4 season, and yet those birds still bred later than in the other areas.

Secondly, the rearing of chicks (the time of greatest food requirement) may be timed to coincide with maximum availability of local food resources as suggested by Trivelpiece and Volkman (1982). Most avian prey, with the exception of *P. georgicus*, becomes available by late October whereas seal material is only available from late November onwards (see Fig. 5). Thus, skuas dependent on seals might be expected to breed later than skuas whose diet consists largely of birds. This is generally the case as the North Valley pairs (the most dependent on seal material) breed later than those in other areas. Within the pairs dependent on avian prey, there is some indication that the timing of breeding of the predominant prey species may influence the timing of the skua breeding cycle. On Gony Ridge (outside the study area) chicks had fledged by the first week of February (suggesting a laying date of early-mid November). The middens in this area showed that the skuas had fed almost exclusively on blue petrels (*Halobaena caerulea*), a very early breeder which arrives by late September and whose chicks fledge by late January. In other areas, where prions and penguins are the main prey, breeding is generally later than on Gony Ridge (Fig. 5). Clearly more detailed investigation of this topic is required, especially regarding the strategy of individual pairs within each area.

Chick growth

While there are some clear differences in chick growth rates between different skua populations, especially the very low value reported by Moors (1980) from the Antipodes Islands, there are quite close similarities between the results of the studies of the two most closely related taxa, *C. lonnbergi* and *C. skua* (Table VII).

Differences in the rate of weight increase presumably reflect environmental circumstances, of which food availability is probably the most important. The rapid growth rate of Bird Island chicks (and notably the 'B' chicks) may have resulted from especially favourable conditions, the 1983/4 season being one of high food availability for skuas (see below).

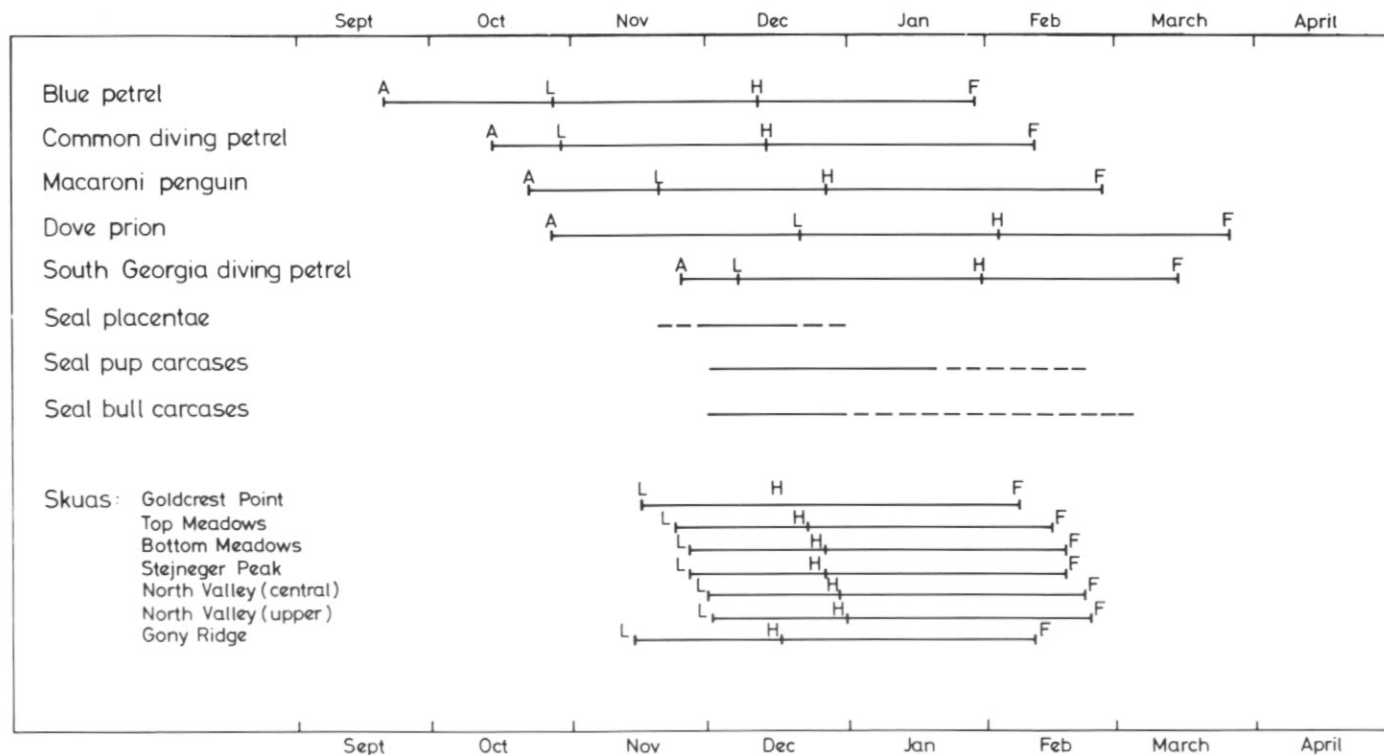


Fig. 5. The timing of the major events in the breeding cycles of the main prey species exploited by skuas on Bird Island, and the timing of the skua breeding cycle in different parts of the study area. The events are referred to as follows: A = approximate date of first arrival, L = mean lay date, H = mean hatching date, F = mean fledging date. In the case of the seals, a solid line denotes the period of maximum availability and a broken line indicates reduced availability. (Sources: Tickell, 1962; Payne and Prince, 1979; Osborne and Copestake, 1983; J. P. Croxall, P. A. Prince, T. S. McCann, unpublished data.)

Table VII. Growth rates of chicks of *Catharacta* skuas from various studies.

Species	Mean weight gain from day 5 to day 20 (g d ⁻¹)	Mean increase in wing length from day 10 to day 30 (mm d ⁻¹)	Source
<i>Catharacta lonnbergi</i>	31.6	—	Moors (1980)
('A' chicks)	45.3	—	Williams (1980)*
('B' chicks)	38.7	—	
(single chicks)	48.9	—	
('A' chicks)	46.9	8.2	This study
('B' chicks)	43.9	7.8	
(single chicks)	45.1	8.4	
<i>Catharacta maccormicki</i>	46.3	8.0	Reid (1966)
('A' chicks)	37.0	9.0	Hemmings (1984)
('B' chicks)	33.3	7.3	
<i>Catharacta skua</i>	42.6	9.3	Furness (1983)

* Day 20–day 30 only.

In the two populations for which comparable data are available for 'A' and 'B' chicks, chicks showing faster weight gain ('A' chicks) also showed faster wing growth (Hemmings, 1984; this study), although there was no general relationship across all studies.

Growth rates of 'A', 'B' and single chicks are similar to those observed by Williams (1980) on Marion Island although he did not find significant differences between the weights of 'A' and 'B' chicks. However, in Williams' (1980) study, a proportion of 'B' chicks did not survive the growth period and this may have biased the remaining sample in favour of the healthier, and presumably heavier, chicks. The present study, where all seven chicks of each category survived to reach a maximum weight, may be a more typical reflection of characteristic weight differences between the two categories of chick.

Breeding success

Overall breeding success (71%) was higher on Bird Island than in many other areas. Burton (1968) recorded 70%, 62% and 46% in three consecutive seasons at Signy Island, Williams (1980) recorded 38.5% and 62% in two years at Marion Island and Barré (1976) found 70% overall breeding success on Îles Crozet. It is possible that on Bird Island the 1983/4 season was particularly favourable for skuas as there was an unusually high mortality of seal pups and of chicks of a variety of bird species (T. S. McCann, P. A. Prince, personal communications) and this may account for the apparently high breeding success of skuas. In normal years their breeding success might be lower, though clearly circumstances are sufficiently favourable generally to allow a steady increase in the breeding population.

As in Burton's (1968) study on Signy Island, overall egg survival was lower than overall chick survival, although this was not the case on Marion Island (Williams, 1980) nor it is necessarily the case with Antarctic skuas (*Catharacta maccormicki*), which show considerable variation in both egg and chick mortality (Hemmings, 1984).

Feeding

The opportunistic feeding habits of skuas are well known, and on Bird Island they use several methods to take a variety of prey. The differences in food remains on middens in different areas suggest some degree of specialization by breeding pairs and, in most cases, this seems to be related to the local availability of resources. Thus the Goldcrest Point skuas feed on the locally very abundant dove prions and diving petrels and also take macaroni penguin eggs and chicks when they are available in the adjacent penguin colony. Skuas in North Valley are much closer to seal beaches, which they exploit extensively. In both cases it is the nearest abundant prey resource that is used most. However, some pairs will occasionally move considerable distances (several hundred metres), often through other skua territories, to exploit restricted but abundant food sources. For example, the Top Meadows middens contained remains of penguins which could only have been acquired by skuas overflying several other occupied territories.

Moors (1980) reports a similarly opportunistic feeding strategy in *C. lonnbergi* at Antipodes Island, where prey items included ten species of procellariiform and one species each of penguin and tern, and species were exploited roughly in proportion to their local abundance. Breeding pairs there, however, appeared to rely even more extensively on prey available on, or very close to, their territory as there was no evidence of, for example, penguin remains on the middens of skuas breeding inland away from the penguin colonies.

Sub-Antarctic islands provide skuas with a considerable variety (both in space and time) of potential prey, a situation well adapted to their opportunistic habits. The influence of this on the breeding behaviour and breeding success of individual pairs is complex and requires detailed further study.

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