BREEDING BIOLOGY OF THE BROWN SKUA, *Catharacta skua lönnbergi* (Mathews), AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

By R. W. Burton

Abstract. About 110 pairs of brown skua (*Catharacta skua lönnbergi*) breed on Signy Island, of which 60–80 have been studied over 7 years. Detailed observations were made on 20–30 pairs over 3 years. The territories are large and nests are widely spaced over the part of the island suitable for nesting. The timing of the breeding cycle varies little from year to year and, except in a few cases, the skuas are extremely tenacious to territory and mate. The nest is made near a roosting site that forms the focal point of the territory. Overall mortality between egg-laying and fledging is 60 per cent on average, most losses occurring in the egg stage. There are no signs of starvation of chicks and few of predation by other skuas. Previous experience of breeding enhances a skua's chance of raising young; experienced skuas are apparently more likely to lay fertile eggs and to incubate them properly.

Many food sources are utilized by skuas on Signy Island, the major one being the broods of penguins. Differences in the breeding biology of subspecies of the great skua are explained as being due to environment.

While serving as a meteorologist at the British Antarctic Survey station on Signy Island (lat. 60°43′S., long. 43°38′W.), South Orkney Islands, I was able to study some aspects of the breeding biology of the brown skua. Agonistic behaviour in the brown skua will be described in a separate paper.

Records of the breeding cycle and nesting habits have been collected sporadically since 1947, but after 1958 ornithological work expanded and a large proportion of the skuas breeding on Signy Island were banded with individual colour combinations and their nests mapped. Since 1960 the chicks have been banded with B.T.O. monel bands instead of the easily lost aluminium bands that had been used previously. This work provided the basis for the present study which lasted from December 1963 to March 1966; 25–30 pairs breeding near the station (the study area in Fig. 1) were visited frequently and occasional visits made elsewhere.

Continuous human occupation of the island since 1947 with the disturbance of banding work and other activities of station personnel is unlikely to have affected breeding. No birds deserted their broods as a result of the disturbance of my own activities; elsewhere, Sladen and others (1966) have reported that skuas have nested for five seasons within a few feet of an occupied station hut. Very few skuas on Signy Island have been killed by men or dogs.

Taxonomic note

Hamilton (1934) studied the forms of the great skua, *Catharacta skua*, in detail and divided the species into five subspecies:

C. s. skua: the great skua of the North Atlantic.
C. s. chilensis: the Chilean skua of South America.
C. s. antarctica: of the Falkland Islands.
C. s. lönnbergi: the brown skua of the sub-Antarctic and Antarctic islands.
C. s. maccormicki: the South Polar skua of the Antarctic continent.

C. s. lönnbergi is the only skua that breeds in the South Orkney Islands, although *C. s. maccormicki* has occasionally been recorded as a visitor.

Habitat and Population

Signy Island, the fourth largest island of the South Orkney Islands group (Fig. 2), has a large area free of ice and snow in summer (Fig. 1), as a result of which about one-third of the South Orkney Islands skuas breed on it. The terrain is rocky, with moraine and scree, but large areas are covered with moss and lichen.

Breeding population. Between 1958 and 1965 the breeding population has ranged between 70 and 110 pairs, of which 60 to 80 on three-quarters of the island have been visited regularly for the banding of adults and chicks. The nests are very scattered when compared with other

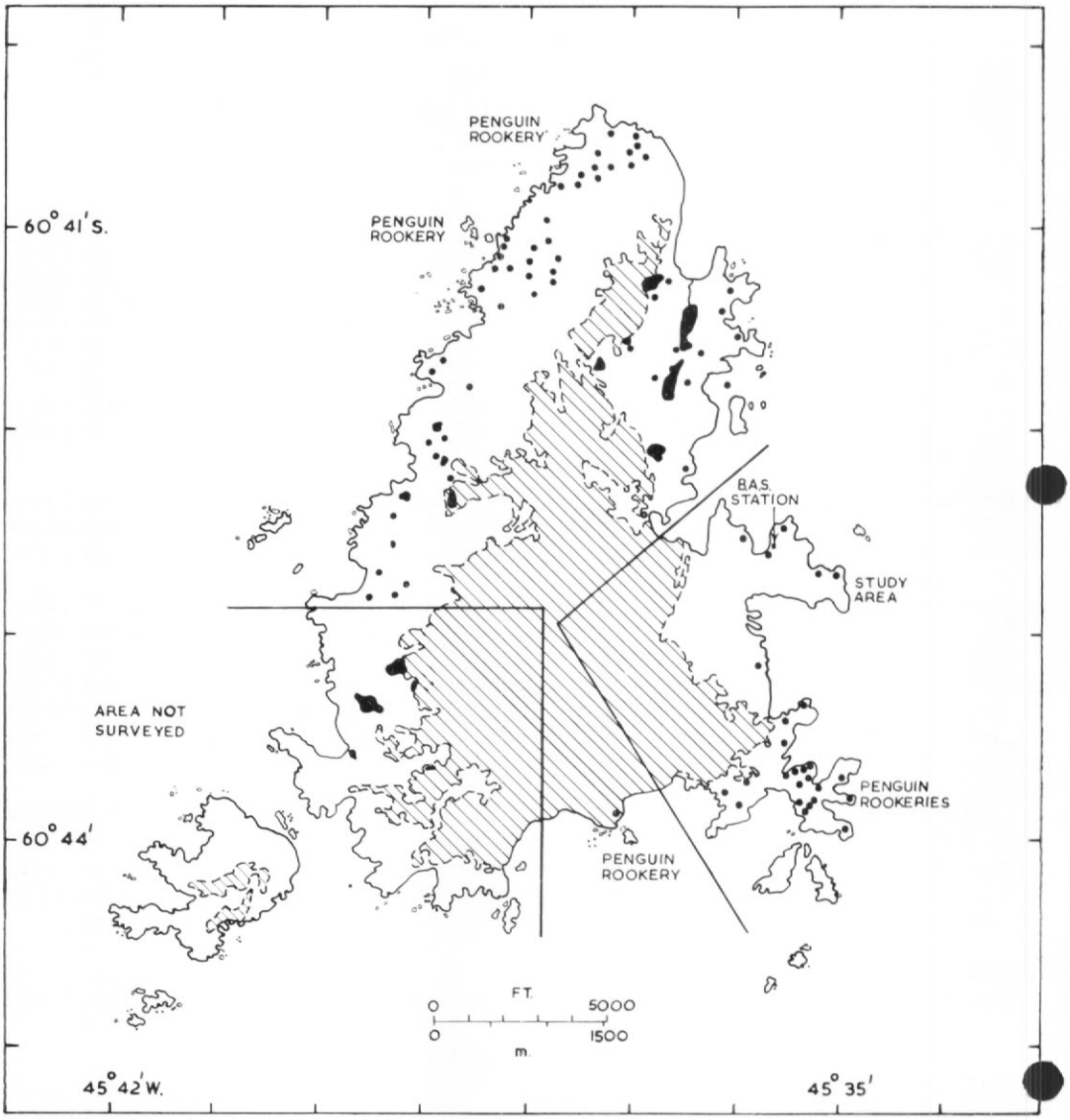


Fig. 1. Map of Signy Island with locations of skua nests indicated by solid circles. The hatched area indicates permanent ice or snow.

skua populations (Table I). There is aggregation of nests around the penguin rookeries, which are a major source of food (Fig. 2), and there may be a certain amount of aggregation due to local topography, but even here the nest density is lower than that of other populations. At Cape Royds, McMurdo Sound, Young (1963*a*) found that territories did not cover the available snow-free area but were concentrated in sheltered areas. Fig. 1 shows that there is no such concentration on Signy Island; in fact, there are more nests on the parts of the island exposed to the prevailing westerlies than in sheltered places. The difference between the two regions may be due to the temperature being lower and the storms being more severe at Cape Royds.

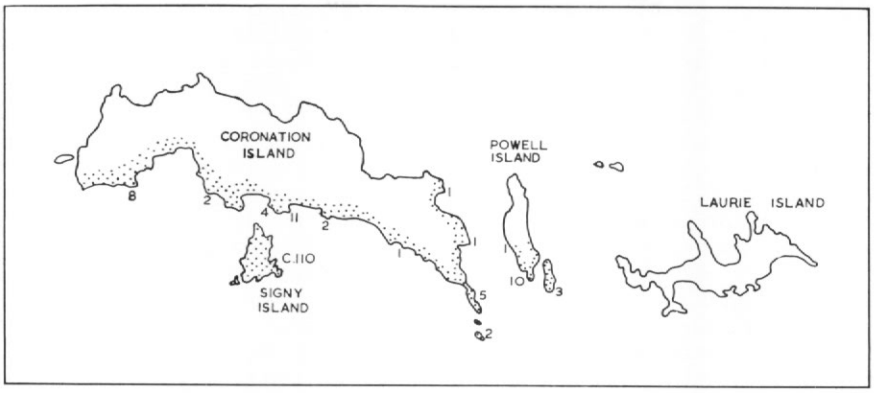


Fig. 2. Map of the South Orkney Islands showing the numbers and locations of skua nests. The stippling indicates the area that has been searched.

Very scanty records kept since 1947 suggest that the breeding population has been relatively stable in numbers until the increase in the last 8 years (Table V). It is not known whether any environmental changes, e.g. in the number of penguins, have been correlated with this increase.

Non-breeding population. Non-breeding skuas gathered in clubs shortly after the breeders established their territories. The clubs are groups of birds that bathe, preen and roost together in certain areas of the island. The members appeared to be resident on the island during the breeding season because banded birds have been recovered several times throughout the summer, and they left the island a month or more after the breeding birds. When not in the clubs the birds were presumably away feeding. Nothing is known of the numbers of non-breeders in the population, for, although up to 70 could be seen at one time, birds were continually joining and leaving the club, and an unknown number must have been away feeding at any instant. At Signy Island breeding skuas were never seen in the clubs as has been observed elsewhere (e.g. Young, 1963*a*).

As monel bands have only been used since 1960, the oldest known-aged skuas to have been recovered in any numbers are at most 4 years old. Recoveries based on the 70 chicks banded each year are: 17 4-year, 14 3-year, five 2-year and one 1-year birds. These figures indicate that the skuas usually return to the area where they were reared when 3 or 4 years old, as they do at Cape Crozier (Sladen and others, 1966). These skuas returned to Signy Island in February and joined the other non-breeding and presumably older birds in the clubs.

TABLE I. SEPARATION* OF NESTS OF THE GREAT SKUA

Distance apart (m.)	*Signy Island*	*Shetland Islands* (Perdeck, 1960)
0–50	0	45
51–100	11	12
101–150	7	
151–200	10	
201–250	12	
251–300	6	
over 300	8	

* The separation of each nest is the distance to its nearest neighbour.

Age at first breeding. At Signy Island the only banded skuas that have returned and held territories and mates are three 7-year olds (which had had their original aluminium bands replaced by monel ones). None of these birds has produced eggs, although two have had territories for 2 years. Great skuas have been recorded as breeding when 4 years old at Fair Isle (Davis, 1962, 1963), and at Cape Royds they usually start to breed at 5 or 6 years but there are records of a 3- and a 4-year skua breeding (personal communication from I. F. Spellerberg). The lack of known-age birds breeding at Signy Island may be due both to the small number of chicks that has been banded and to the possibility that they may have nested elsewhere in the South Orkney Islands where they would not be recovered.

Mortality and expectancy of further life. Using the colour-banding of breeding birds and sight-recoveries, it is possible to estimate the annual mortality and mean life span of breeding skuas on Signy Island. The proportion of the breeding population that has been banded has varied from year to year, but in all years (except 1959) every pair in the surveyed part of the island was checked for colour bands. Data on survival from 1960 onwards are given in Table II. A mortality of 9 per cent/yr. and a mean adult breeding span of 11 years are acceptable with the recorded 61 per cent of eggs producing fledglings (p. 20).

TABLE II. SURVIVAL ESTIMATES OF BREEDING SKUAS AT SIGNY ISLAND (BASED ON COLOUR-BANDING)

Year of banding	*Known minimum period of survival* (yr.)						*Accumulated total at risk*
	1	2	3	4	5	6	
1958	22	19	18	15	15	14	22
1959							
1960	36	30	27	22	19		58
1961	112	96	88	75			170
1962	107	94	78				277
1963	95	79					372
1964	80						452
TOTAL	452	318	211	112	34	14	

Mean survival = 91 per cent (range 90–93 per cent).
Mean mortality = 9 per cent (range 7–10 per cent).
Therefore, mean life span, $(2-m)/2m$ = 11 yr.

BREEDING CYCLE

Certain aspects of the breeding cycle have been described by other authors, i.e. Eklund (1961) and Young (1963*a*, *b*) on *C. s. maccormicki*, Perry (1948) on *C. s. skua* and Stonehouse (1956) on *C. s. lönnbergi*. As there is little variation in the breeding cycle of different subspecies, a full description of these aspects will not be repeated here.

The nests in the study area were visited as often as possible, from twice a day to twice a week, to record the state of the brood and the presence of adults. The sex of a few individuals was determined by observations of courtship behaviour or by dissection.

Arrival at the breeding area. Observations of 13 years show that skuas appear at Signy Island in the second week of October but in three other years the first arrival was recorded in September, the earliest being on 2 September. Skuas return to South Georgia, 500 miles (800 km.) north of Signy Island, a month earlier (Stonehouse, 1956), so they may move south as conditions in the Southern Ocean ameliorate, but on the other hand, they arrive at the Antarctic continent, some 800 miles (1,290 km.) farther south at about the same time as at Signy Island (Eklund, 1961).

There is no evidence as to whether skuas with previous breeding experience arrive earlier

than others, although those with 1 year's experience take up terrritories later than those with more than 1 year's experience.

Pair formation. Known breeding birds could be seen around the island for a few days before taking up their old territories, which were defended by displays and attacks on intruding skuas almost immediately. Sometimes both members of a previous year's pair returned on the same day but often one, either the male or the female, arrived up to a fortnight earlier (Fig. 3) and defended the territory.

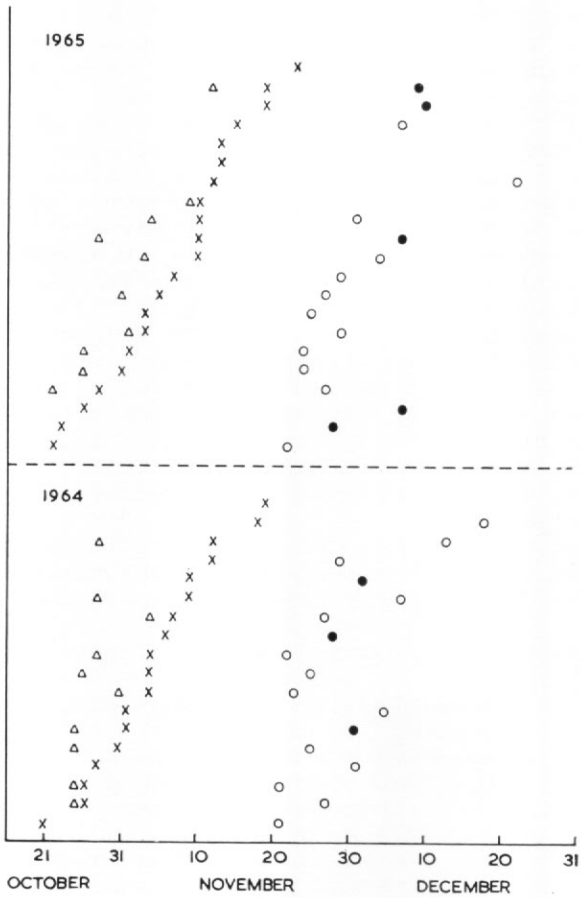


Fig. 3. Dates of pair formation and egg-laying in two different years for pairs in the study area. × represents pair formation and △ the arrival of one member of a pair if different from the second. ○ represents egg-laying of "experienced" pairs and ● egg-laying of "inexperienced" pairs.

Pair formation is spread over a month (Fig. 3) and past records indicate that the date of the first pair formation varies by only a few days from year to year. Nothing is known about variation in the dates of maximum pair formation. If the previous year's mate returns late, the first arrival of a pair will often associate with another skua. This is a simple process; a skua lands by a territory owner, both give the "oblique-cum-long call" (Monyihan, 1962) and stand side by side. I saw no sign of marked hostility between the two birds at these times. The new bird did not join in defending the territory for a few days, although I do not know whether it does so when it is alone in the territory while the established owner is away foraging. A skua sometimes had several temporary partners over a short period before one became permanent.

One established breeder was seen with two different birds in 1 day and over 3 weeks at least seven different birds kept company with it. In these situations it is not known whether the male or female rejected the partnership. On the return of the old mate the temporary partner disappeared but, if the former did not return, the temporary partner became the new mate and breeding took place. Nine times between 1962 and 1965 one member of a pair was recorded as staying away from the island for one season and returning the next. In the interval its mate took a new partner, which was displaced when the original returned. On four occasions the male of one pair and the female of a neighbouring pair have failed to return. Their mates paired and nested in one or other of the territories. On two of these occasions the missing birds turned up again a year later and mated together, taking up the vacant territory. These new partnerships were permanent and were the only instances of changes of mate, apart from those due to the death or temporary absence of one member of a pair.

Polygamy. Bonner (1964) reported a case at South Georgia of one male skua mating with two females, both of whom laid eggs in one nest. There have been two such cases at Signy Island. One trio lasted for one season but the other was in existence in 1958 when records started and was still extant in 1965, although two of the original members have been replaced. Whenever one of them disappeared, presumably having died, another bird joined. The new birds had not bred elsewhere previously as far as is known. It seems likely that this trio also consists of one male and two females, because in one year four eggs were found in the nest. They are usually successful in rearing chicks to fledging, but in two years all the eggs were lost. When there are more than two eggs in the nest, it is likely that at any one time not all the eggs could be fitted into the two brood patches of the incubating bird and so could chill.

Courtship. Courtship feeding was rarely observed and copulation only once. These behaviour patterns have been fully described by Moynihan (1962) for *C. s. chilensis*. The behaviour of *C. s. lönnbergi* does not differ from that of other subspecies of skua that have been described. A possible explanation for the rarity of observations of courtship feeding may be that the pairs that were watched frequently were feeding mainly at nearby penguin rookeries where the female could easily forage for herself.

Preliminary activities of pairing were seen frequently in the clubs and consisted of the "circular parading" described by Moynihan (1962). "Circular parading" by territory owners was never seen. The only form of greeting ceremony observed consisted of the "oblique-cum-long call".

Throughout the breeding season a skua might be joined by another when its mate was away foraging.

Territories. The territories defended by skuas are primarily resting and breeding places, and skuas feed there only if food happens to be available.

The one or two roosting sites (Stonehouse, 1956) form the focal points of the territories. A roosting site may be on a 50 m. knoll or on a small rock, depending on the terrain. The important feature is that the skua has a good view of its territory and is easily visible to other skuas. At the beginning of the season a pair of skuas is first found at the roosting site, and it seems that the rest of the territory is formed around this focus (though with the large territories on Signy Island it was not possible to observe any behaviour that would provide evidence for this (Fig. 4)).

Nest hollows are made near the roosting sites and their location varies by only a few metres from year to year, except when there is a change of roosting site, in which case the nest site is moved as well. The proximity of nest to roosting site causes some aggregation of nests as several pairs may roost on the same knoll. Thus, although the territories may be over a hectare in size, the nests are grouped together near the mutual boundaries.

The skuas concentrate breeding activities and defence in a small part of the territory around the nest and roosting sites. This area is about 30–50 m. in radius, irrespective of territory size. Outlying parts of the territory are only visited if intruders land there or if food is available, so unless this central area of one pair is contiguous with that of another, the territory boundaries are ill-defined. When these areas are very widely spaced, there are neutral zones between the territories.

The territories on Signy Island have varied little since mapping started in 1958. Changes of roosting and nest sites have rarely resulted in a shifting of territorial boundaries. Territories

Fig. 4. Skua displaying on a roosting site.

are usually taken over by new pairs as soon as they are abandoned. In one instance, a new pair formed in a territory a day after it was abandoned in late January. Other new pairs form territories in neutral zones between territories or in the outer parts of large established territories, apparently with little opposition from the original owners.

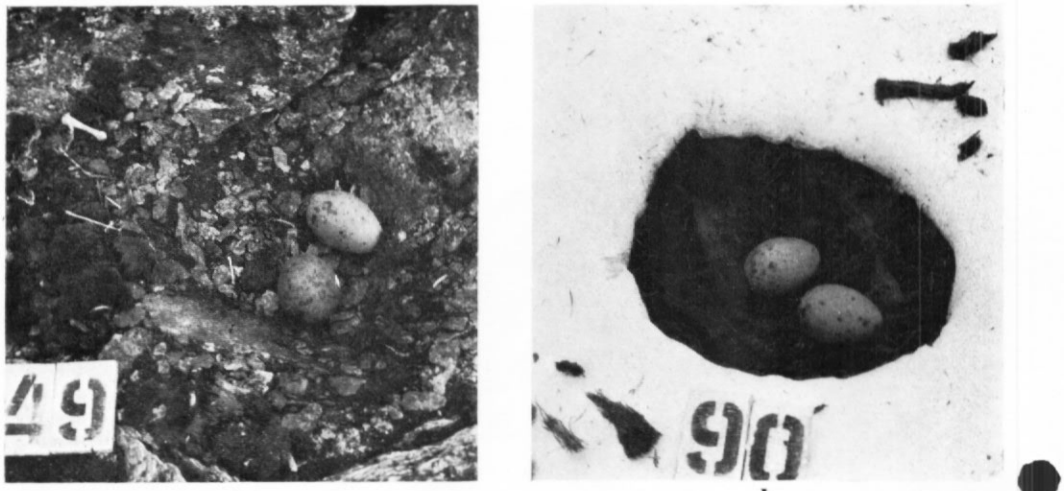
Nest-making. The nest is always on a flat area, the smallest recorded on Signy Island being a cliff ledge of about 50 m.^{2}. They are never made in hollows, for, although these would provide shelter, they are the places where snowdrifts that accumulate in winter persist well into the summer. Nests are sometimes made through a few centimetres of snow but the skuas never attempted to excavate through anything deeper.

Nests are made on a variety of substrates, the most usual being moss or lichen which is torn out and pressed down to form a scoop, which is sometimes lined with the same material. Nests are also made in gravel and compacted sand, and very occasionally on rock where a circle of lichen is scraped away. Scoops on the last two types of substrate have never been seen in use (Fig. 5a, b).

Several scoops may be made, or only one. Some pairs also make an extra scoop after the chicks have left the original one. These are sometimes used as resting places by the chicks but not apparently in preference to any other small depression in the ground.

Egg-laying. Eggs are laid about 3 weeks after pair formation (Fig. 3), the first being found in the last week of November (in 10 year's observations the spread has been from 21 to 29 November). Over half the clutches are started within a week of the first and the rest usually within the next 2 weeks, but some may be started as much as 8 weeks later (mid-February). Although skuas return to South Georgia a month earlier than to Signy Island, birds at both places lay at about the same time. This, with only slight annual variation in laying date at Signy Island, suggests that the onset of laying in skuas is independent of climate.

The first egg was laid 2 days after the nest scoop was made, and the second 2 days later. Stonehouse (1956) has said that the female skua becomes less active and is rarely seen away



a b

Fig. 5. a. Unlined skua nest on pebbly ground.
b. Lined nest on snow-covered moss. Lumps of moss have been torn out to form the scoop and some have then been pressed down to form a lining.

from the centre of the territory from just before egg-laying until the clutch is complete, but I saw no sign of this. All the clutches I found were of two eggs, except one with only one egg. It is unlikely that this latter was due to the loss of a second egg, because in other cases of this the remains of the egg were always found near the nest. Only the trio laid more than two eggs in one nest.

If the first egg is lost, two more are laid, but if the complete clutch is lost, then no more are laid that year. The third replacement egg is laid 2 days after the second if the birds are incubating normally. If an egg is lost because it is not incubated, a new nest is made and the clutch re-started after an interval of a few days.

The few inexperienced pairs studied (those with one member breeding for the first time) did not always lay after experienced pairs (those with two birds who had bred for at least 1 year previously) (Fig. 3). New pairs often did not lay in their first (and sometimes second) season, but if they did, they nearly always laid later than other pairs. Of the 15 pairs (ten of which were "inexperienced") known to have laid 20 or more days after the first pair of the season, only seven raised chicks to fledging. This was a lower success rate than the rest of the population (Table V) and was due mainly to the eggs being neglected and eaten soon after being laid. Thus, there is little evidence that late egg-laying is due to lack of previous breeding experience, but late laying is correlated with a failure to raise fledglings.

Incubation period. Full incubation may not start immediately, since the first egg of a clutch was sometimes cold to the touch. However, after the second egg had been laid, the clutch was rarely left uncovered, apart from short periods during takeover of incubation (for description see Young (1963*a*)), when the sitting bird (Fig. 6) left to defaecate or during courtship feeding which always took place away from the nest.

I was able to get nine estimates of the time spent incubating, ranging from 1 hr. to 2 hr. 30 min., the average being 1 hr. 55 min. This is less than the average of incubation stints observed by Young (1963*a*) and Eklund (1961). Between incubation stints the skuas spent most of their time standing or sitting at the roosting site. At the three nests observed from the hide, the birds foraged in nearby penguin rookeries and they were away from the nest or roosting site for only about 15 to 30 min. At nests distant from a penguin rookery, the birds spent longer foraging but they still spent a large part of the "off-duty" period in the territory, so the length of the incubation stint is not related to foraging time.

16 eggs took an average of 30½ days from laying to hatching (range 29–31 days). Chipping

Fig. 6. Skua settling on its nest.

starts 2 days before the chick emerges. These figures are within the range of those quoted for other skua populations. The difference between hatching dates of the two eggs of a clutch is the same as that between laying dates, so that development of the first egg is not retarded by its shorter incubation. Eggs that did not hatch were incubated for up to a week more, then eaten.

On several occasions eggs were found outside the nest hollow. Even if then placed by hand on the rim of the scoop they were not rolled back into the nest but eaten. To test whether skuas have the ability to roll eggs into the nest with the bill, as do certain other ground nesters, e.g. black-headed gulls (*Larus ridibundus*) (Beer, 1962), eggs were taken out of the nest and the behaviour of the skuas watched from a distance. It was only possible to stimulate egg-rolling if both eggs were removed from the nest and placed not more than about 10 cm. from the rim. Otherwise the skua sat in the empty nest and ignored the eggs, except in a few instances when it sat on the eggs where they were. Although these tests were few in number and incidental to the main work, it would seem that the egg-retrieving capacities of skuas are not as well developed as those of the black-headed gulls studied by Beer.

Nestling period

Egg-shell removal. Like many other ground-nesting species, skuas remove egg-shells from the nest after the chicks have hatched. From the few observations made, the skuas had generally removed egg-shells by about 2 days after the chick had hatched, although one shell was recorded as not being removed for 9 days. The shells were moved a distance of a few centimetres to a few metres at one time. The ones that were found only a short distance from the nest were moved further at a later date.

Tinbergen and others (1962) have shown that black-headed gulls remove egg-shells fairly promptly after the chick has emerged, but not immediately after emergence. This is due to two conflicting pressures. Prompt egg-shell removal decreases the chance of interspecific predators being attracted to the nest, but by leaving the nest with the egg-shell the adult gull

exposes the vulnerable wet chick to predation by neighbouring black-headed gulls. Sabine's gull (*Xema sabini*), which, unlike the black-headed gull, nests quite far from its neighbours (Brown and others, 1967), removes egg-shells while the chick is wet. Brown and his co-workers have suggested that in this situation predation from other species is greater and from the same species is less. Yet great skuas also nest at a distance from each other, and egg-shell removal seems to be delayed. The skua nests on Signy Island are unusually widely spaced (Table I), so predation by neighbouring skuas may be less than in denser populations where the delay of shell removal may be important.

Care of the chicks. The chicks dry out within a few hours of hatching and may leave the nest in the first 24 hr., but for most of the time they are brooded by the parents. This becomes less frequent after the chicks are 1 week old, occurring at intervals until they are 2 weeks old. The chicks always returned to the nest to be brooded. Females brooded the chicks more often than the males, and when not brooding they usually stood near the chicks, whereas the males would stand on the roosting site.

Either of the parents or a chick may take the initiative for brooding. A chick will run to a sitting adult and, squealing, attempt to crawl under it. Sometimes the adult objects, lunging at the chick with open bill and finally moving away. If willing to brood, the adult walks to the nest followed by the chick. At other times the adult will walk over to the nest and stand over it until the chick runs underneath. On one such occasion the adult stood with wings open uttering "alarm calls" until the chicks had run to it. This was the only time that the chicks were seen definitely to respond to calls by the parents, yet there were no intruders about and the adult was looking at the chicks.

Brooding did not appear to be correlated with weather. Chicks a few days old were often left exposed in heavy rain but brooded on calm sunny days. Young (1963*a*) found a correlation between brooding and low temperatures, but there were no extremes of low temperature at Signy Island during this period.

Brooding always takes place in the nest scoop, although one chick was brooded in a nest that had been made prior to that in which the eggs had been laid. When brooding ceased, the nests were ignored and the chicks lay up in natural depressions in the ground or in the angle formed between the ground and a rock. These roosts became very conspicuous with droppings, whereas the original nest remained clear, indicating that the chicks did not defaecate at the nest.

When 3 weeks old the chicks became more active, wandering around the nest area, playing with penguin egg-shells and occasionally hopping and flapping their wings. At about this time they emit a low-pitched whistle (Stonehouse, 1956), different from the squeal with which they attracted the parents' attention when they were very young. Stonehouse has described how the adult will leave food when the chick approaches whistling. This was not seen to occur during this study. Chicks were often heard whistling as they roamed around the nest area, while the parents stood by apparently taking no notice.

Not all chicks stayed near the original nest; some moved up to 100 yd. (91 m.) away, usually towards a roosting site where rocky ground provided more cover (Fig. 7).

No sign was seen of siblings fighting as reported by other authors (e.g. Young, 1963*a*; Reid, 1966). Siblings could be found lying side by side from hatching to fledging.

After the chicks were about 1 month old the parents spent more time away from the territory and often both were away at the same time. As breeding birds were never seen at the clubs or elsewhere around the island except at penguin rookeries, this may be due to an increased time needed for foraging. Certainly, it seemed more difficult to obtain food from the penguin rookeries as the latters' chicks were half grown and difficult for the skuas to kill (p. 24). At this age the skua chicks seemed well able to defend themselves in their parents' absence. An intruding skua that attempted to molest them would be driven away by the chicks who would rush forward squealing. They never attacked their own parents, indicating that they can distinguish them from strangers.

Feeding the chicks. The chicks were first fed within 24 hr. of hatching, both parents taking an equal share, although the male appeared to make more foraging flights. Feeding did not always occur after an adult returned from foraging, and it often occurred when the adult had not foraged for some time. The chick was led away from the nest by the parent, who regurgitated food on to the ground, picked up pieces and held them in the tip of its bill for the chick to

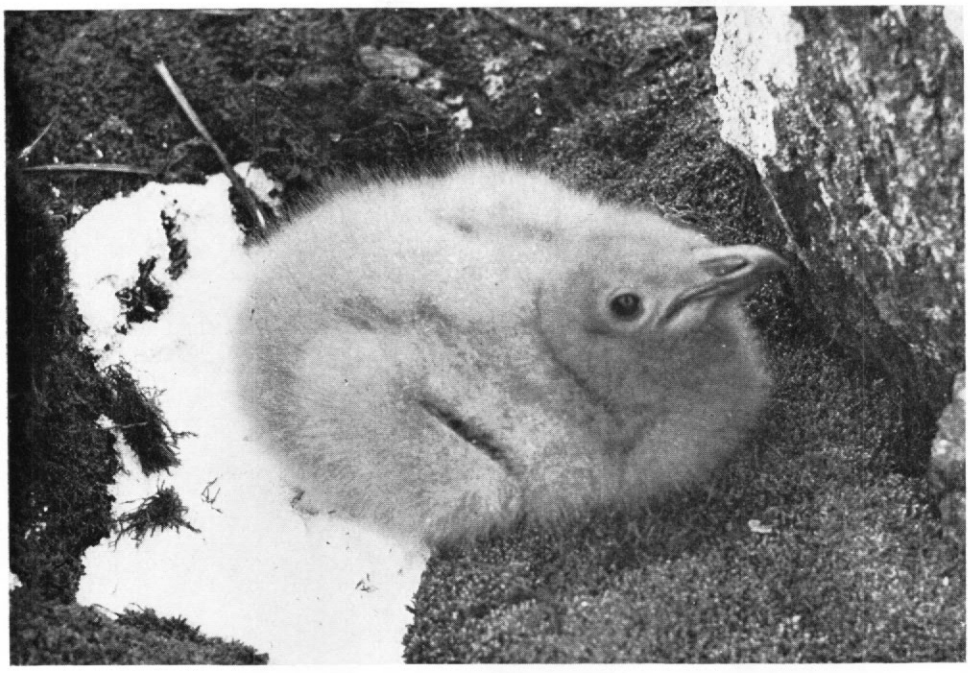


Fig. 7. A 2-week old skua chick.

peck. Judging by what could be seen of food being disgorged by the parents and from food that was disgorged by chicks when being banded, the parents did not pre-digest the food before giving it to the chicks. The other parent often joined in feeding the chick and assisted in tearing up the food, but it might feed itself without giving any to the chick. It might even take food from the first parent's bill. When the chick was a fortnight old, it no longer took food from the parent's bill but was able to take it directly from the ground.

As with brooding, either parents or chick took the initiative in feeding. The parent might walk up to the chicks without any call (cf. Young, 1963*b*) and regurgitate, or the chick would run squealing to the parent with head withdrawn in the adult submissive posture and peck at the parent's bill, often violently so the parent had to run away from the chick in order to regurgitate. Soliciting and regurgitation were not always elicited by the behaviour of the other party. Occasionally a chick took no notice of the parent's attempt to regurgitate, and the parent might drive a soliciting chick away.

Juvenile stage. The chicks started to fly when about 60 days old, but they continued to run from danger rather than fly until they had fully mastered take-off and landing about 2 weeks later. After this, the parent's interest in them diminished. Human intruders were not attacked so vigorously by the parents, who also did not go to the aid of flying juveniles that were being attacked by other skuas, despite the former's squeals. In two cases juveniles strayed into a neighbouring territory and stayed there for several days until they finally left the island. It is not known whether the juveniles were adopted by the neighbouring adults as Young (1963*a*) observed, or whether the territory boundaries had lost their significance.

Departure from the territory. The juveniles stayed in the territory for 3 or 4 weeks after they had started to fly, usually leaving in the second or third week of March. One parent stayed with the juveniles until they left, or for a day or two after, but the other left the island a few days before them. This was the female in eight pairs whose sexes were known and in four pairs at South Georgia (Stonehouse, 1956). After they left the territory neither adults nor juveniles were seen again during the season, so they must have dispersed straight out to sea. It is not known whether the juveniles start to forage for themselves when they leave the territory.

Breeding Success

The success of the pairs in the study area, as measured by the percentage of eggs reared to fledging, was 59 per cent over three seasons, with the greatest loss in the egg stage (Table III). Breeding success on the surveyed part of the island has been recorded over 7 years (Table V), showing an average annual rate of 61 per cent for pairs that laid. Occasional observations show that the proportionate loss of eggs and chicks on the rest of the surveyed part of the island was not significantly different from nests in the study area.

Table III. Number of pairs of skuas and their breeding success in the study area (over 3 yr.)

	1963	1964	1965	*Percentage of total*
Number of pairs	23	32	26	
Number of pairs that laid	22	24	19	
Number of eggs laid	43	48	37	
Number of chicks hatching	31	33	21	
Percentage hatch	72	69	57	66
Number of chicks that fledged	30	30	17	
Percentage of chicks that fledged	96	91	81	90
Breeding success (percentage of chicks fledged from eggs laid)	70	62	46	59

Causes of loss

Eggs. It was not always possible to ascertain the cause of loss, as an egg might disappear without trace between two successive visits to the nest. Eggs found outside the nest had been lifted out in the plumage of the sitting skua when it flew straight off the nest as, for instance, when it left to defaecate. In some instances these were known to be cracked or addled, in which case they would be lighter and more likely to adhere to the plumage. Eggs that failed to hatch and were abandoned could have been infertile or their embryos may have been killed by chilling at some stage. There was no instance of eggs being abandoned once incubation was under way. Table IV shows that the main cause of loss was failure to incubate after the eggs had been laid. The figure given does not include four eggs that were lost and replaced.

Chicks. The two chicks found dead in the nest (Table IV) were no more than 2 days old. There was no sign of injury so perhaps they were smothered under the parent. Death of two siblings was due to one of the parents dying. It is not known whether they were killed for food by the weak parent before its death or whether intruding skuas killed them while the other parent was away. The remaining chicks disappeared, presumably having been taken by intruding skuas.

Factors affecting breeding success

Food supply. As discussed on p. 25, there was an abundance of food available from penguin rookeries and several other sources throughout most of the breeding cycle. As the adult skuas spent much time roosting, it seems that they were not under a strain to get enough food for their chicks and there was no sign of the latter starving.

Weather. Heavy snowfalls are rare at Signy Island during the summer and during the three seasons of the study the weather during the incubation period was usually calm with little precipitation. Eggs were known to hatch after at least 20 min. exposure to 15 kt. (7·7 m./sec.) winds with the air temperature just below freezing. Pinder (1961) found the corpse of a skua

TABLE IV. CAUSES OF LOSS OF EGGS AND CHICKS IN THE STUDY AREA, 1963-65

Causes of egg loss	*Number laid*	*Not incubated*	*Accidentally lifted out of nest*	*Shell broken*	*Failed to hatch*	*Unknown*	*Total*	*Percentage loss*
	127	14*	9	4	11	8	46	36

Causes of chick loss	*Number hatched*	*Dead in nest*	*Eaten by parents*	*Unknown*	*Total*	*Percentage loss*
	81	2	2	4	8	10

* Does not include eggs lost and replaced.

chick half buried in snow after a heavy fall, and the next year Jones and Pinder (1962) reported that after a heavy snowfall in early December they found two nests buried. At one of these, an adult was still sitting although buried completely.

Storms at Signy Island were not severe enough to prevent adults from foraging or to cause the death of chicks by chilling.

Predation. Predation of chicks by other skuas was rare. This might have been due both to the abundance of food from other sources and to the large territories which would prevent skuas from getting near the brood without evoking response from the parents.

Experience of parents. Table V, in which the percentage of successful eggs is given, shows

TABLE V. ANNUAL POPULATION AND BREEDING SUCCESS

Year	*Total pairs*	*Number of pairs that laid*	*Percentage* success of total pairs*	*Percentage* success of pairs that laid*	*Percentage of pairs with new birds*
1958	59	59	63	63	
1959	—	—	—	—	
1960	63	62	60	60	
1961	68	67	58	59	23
1962	64	58	64	71	14
1963	67	60	59	66	16
1964	84	71	47	55	25
1965	81	66	43	53	28
Average			56	61	

* Percentage of eggs laid that gave rise to fledglings.

that as the total number of pairs of skuas on Signy Island has risen the success has decreased ($p = 0{\cdot}015$; Kendall rank correlation). This is partly due to an increase in the proportion of pairs that did not lay ($p = 0{\cdot}015$), but the correlation still holds if these are omitted, since there was a lower success, as population rose, in pairs that did breed ($p = 0{\cdot}035$). The detailed figures for the last 5 years suggest that this is linked with the proportion of skuas without previous breeding experience that have joined the breeding population as it increased. Records for 5 years, summarized in Table VI, show that pairs, including one bird that has not paired in previous seasons ("inexperienced" pairs), are not only less likely to lay than those in which both members have been paired in previous years ("experienced" pairs), but if they do lay they are less likely to rear their young. The few records available show that success of 20 pairs in their second season is 17 per cent higher on average than that of their first season, and only 2 per cent higher in their third. It has been shown that chick loss is small, so it seems that the effect of inexperience is due to a failure to incubate properly and to laying of infertile eggs.

Comparison with other populations. In no years were the successes at Signy Island as low as those that have been recorded elsewhere in the Antarctic (Table VII), but they are comparable

TABLE VI. EFFECT OF EXPERIENCE ON EGG-LAYING AND BREEDING SUCCESS AT SIGNY ISLAND, 1961–65 (BASED ON COLOUR-BANDED BIRDS)

	Number of pairs that failed to lay	*Number of pairs that laid*	*Percentage chicks fledged from eggs laid*
"Experienced" pairs	5	133	71
"Inexperienced" pairs	26	115	52

TABLE VII. BREEDING SUCCESS AND NEST DENSITY OF GREAT SKUA AT DIFFERENT LOCALITIES

Location	*Date*	*Number of pairs*	*Percentage breeding success*	*Nest density*	*Authority*
Cape Hallett	?	?	21	High	Reid quoted by Young (1963*a*)
Cape Royds	1959	67	23	High	Young (1963*a*)
Windmill Islands	1957	40	47	High	Eklund (1961)
Shetland Islands*	1946	149	51	High	Perry (1948)
Heard Island	1951	30	58	Low	Downes and others (1959)
Signy Island	1958–65	50–80	average 61	Low	This study
Fair Isle*	1952–56	8–17	average 66	Low	Williamson (1957)

* Northern Hemisphere.

with some of those for other localities. Young (1963*a*) has suggested that there is a correlation between success and territory size. Figures for nest density are not always available but Table VII shows that as nest density decreases success increases. Since it would be less easy for intruding skuas to get near the brood without evoking hostility from the parents when territories are large, widely spaced nests would decrease chances of predation of chicks. Young (1963*a*) found that chicks weakened through starvation were more likely to be preyed upon, and the inability of adults to forage at sea in bad weather might lead to their attempting to prey on skua chicks. At Signy Island inability to forage and consequent starvation of chicks did not occur.

Feeding Habits

Methods of obtaining food

Thieving. Skuas were sometimes seen to chase a Dominican gull (*Larus dominicanus*) and take food, for example, a fish or Wilson's storm petrel (*Oceanites oceanicus*), from the latter's bill, although the gull would sometimes retrieve its prey from the skua. Giant petrels (*Macronectes giganteus*) have been reported as being harried by skuas to make them disgorge their food. At the Argentine Islands (lat. 65°15′S., long. 64°16′W.), blue-eyed shags (*Phallacrocorax atriceps*) are the target of skuas' thieving (Smith, 1960), but apparently not at Signy Island although the shag is common there and was subjected to close scrutiny (personal communication from C. A. J. Howie). Skuas appeared to restrict this thieving to larger species, for there are no records of the smaller petrels or the Antarctic tern (*Sterna vittata*), which carries food in its bill, being molested in this way. The incidence of thieving varies between populations and it is an opportunist form of feeding. No skuas perform this regularly so it is an unimportant method of obtaining food, at least in the Antarctic.

Scavenging. Skuas will eat any carrion that is available and they will search the shoreline for marine invertebrates.

Fishing. Although skuas fed their chicks on fish, fishing has never been observed at Signy Island, so it presumably took place some distance from the shore. The method of fishing by plunge-diving has been described by Young (1963*b*).

Predation of other species

Eggs. Any eggs that have been deserted, either temporarily or permanently, will be taken, but usually eggs are well guarded by the parents. Skuas could be seen hovering or wheeling over penguin rookeries, then diving down into the rookery to fly up a few seconds later with an egg in the bill. The egg would be carried away from the neighbourhood of the penguins to be consumed at leisure by pecking a hole in the shell and sipping the contents.

Young. Newly hatched chicks were not often taken as they were usually brooded by the parents. However, after brooding has ended the young of all species at Signy Island are left in or near the nest while the parents are away feeding. It is then that they fall victims to skuas. Young of the hole-nesting petrels have a certain immunity but skuas were frequently observed putting their heads down holes and crevices. If these were in rocks, the skuas would not be able to reach the occupants, but dove prions (*Pachyptila desolata*) sometimes burrowed in moss banks, which could be excavated by the skuas. Penguin chicks were usually safe when in the crèches but, if a chick became separated from the others, the skuas would drag it by the head away from the vicinity of the adult penguins which might attack. Usually it was weak chicks that were caught in this way, but occasionally healthy ones were taken. The skua would drag the chick until it fell over, then straddle it and peck and tear the neck until the chick was helpless. Juveniles of petrels were taken when they started to fly, the skuas catching them with their bills and landing to kill them.

Adults. Skuas rarely captured healthy adult birds except for members of the hole-nesting species, that is snow petrels (*Pagadroma nivea*), Wilson's storm petrels and dove prions. These species were usually caught on the ground outside their nest holes when they came back from feeding. Adult cape pigeons were taken less frequently than the other small petrels, which may be due to their nesting on cliff ledges. Whereas other petrels land near their nest holes and walk with difficulty up to the entrance, when they are vulnerable to skuas, cape pigeons fly

straight on to the nest ledge where the skuas have difficulty landing. The storm petrels were the only adult birds observed being caught while flying; they are small enough to be taken in a skua's bill and swallowed whole.

Skuas do not appear to have any predominant method of feeding. They are opportunists, taking advantage of what is available. The plunge-diving technique is used by many birds and the skuas have no adaptation for other methods except to investigate any possible source of food and, perhaps, a bill that is adapted for tearing flesh. That they are not well adapted for flesh-eating, in the same sense as other predatory birds, is shown by the failure to hold food down with the feet. They take the food in the bill and pull backwards until a piece is ripped off. This is easy if the food object is heavy, for example, a seal carcass, but a skua will take a long time to dispose of a petrel, unless it is aided by another skua pulling in the opposite direction.

Food taken. Skuas utilized every source of food material on Signy Island except terrestrial and fresh-water invertebrates. Quantitative investigation of the abundance of the various sources and the extent to which the skuas utilized them was not possible.

The chicks and eggs of penguins formed the major supply of food for skuas on Signy Island, and to some extent this affected the distribution of skua nests (Fig. 2), although each was often found without the other, for example, on Coronation Island there are penguin rookeries without adjacent skuas' nests despite suitable terrain for the latter. Every pair of skuas on Signy Island fed to some extent on the broods of penguins. Skuas with penguin rookeries in their territories fed on little else but, because of the large size of the rookeries, these pairs could not defend their territories to the exclusion of others. Young (1963*a*) estimated the availability of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*) as food for skuas at Cape Royds. He found that for a short period after laying had started the penguins lost many eggs to skuas, but this supply diminished when the penguins settled down to incubation. After hatching, the chicks were relatively safe until the parents stopped brooding them. These young chicks fell an easy prey to skuas, but after they reached the crèche stage they could only be taken easily by skuas if they were weak. Young showed that the flush of penguin chicks lessened when the skua chicks were still very young and so were of limited value as a source of food. At Signy Island there were equal numbers of chinstrap penguins (*Pygoscelis antarctica*) which bred a month later than the Adélie penguins (Fig. 8). (There was also a smaller number of gentoo penguins (*Pygoscelis papua*) breeding at the same time as the Adélie penguins.) The flush of chinstrap penguin chicks occurred when the skua chicks were growing rapidly and it

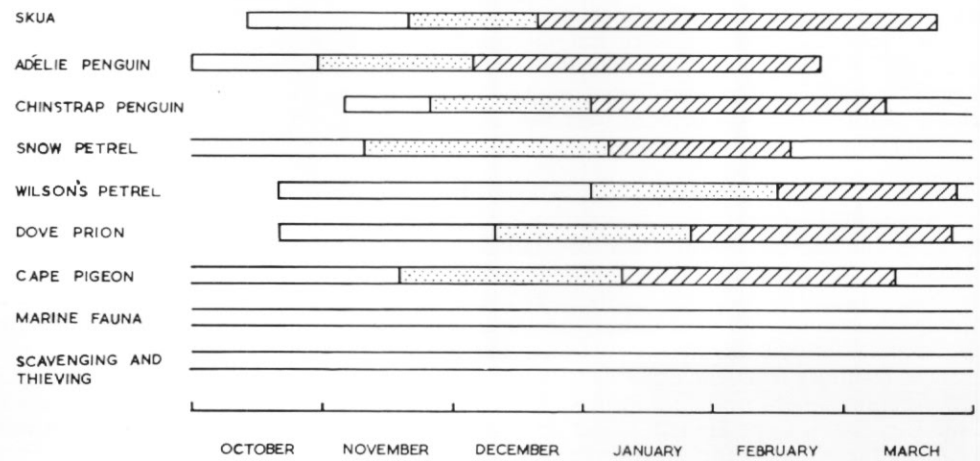


Fig. 8. Availability of different sources of food in relation to the skua breeding cycle. Stippling indicates eggs and oblique hatching indicates chicks.

was only when the latter were nearly full grown that their parents had to forage elsewhere. As mentioned earlier, skua chicks are able to defend themselves at this stage and both parents can forage at the same time.

There were about 3,000 pairs of penguins to each pair of skuas at Signy Island. This ratio varies around the Antarctic, from 70 : 1 at the Windmill Islands (Eklund, 1961) to 5,000 : 1 at Hope Bay, at the north of the Antarctic Peninsula (Sladen, 1958). The relationship between skua and penguin populations in different places cannot be directly compared, as the size of a rookery affects the number of skuas that can forage in it. Small rookeries can be defended by a pair of penguins, as at Cape Royds (Young, 1963*b*), but large ones, as at Hope Bay and Signy Island, are accessible to all skuas. The size of the rookery also affects the abundance of food available from them, as large rookeries have more penguins nesting on the margins where they are more vulnerable to skuas.

Skuas may take fish and Crustacea throughout the breeding season, but not in quantity until the supply of penguin chicks begins to fail. Outside the breeding season, when the skuas become pelagic, they must be dependent on organisms near the surface.

Thieving and scavenging occur sporadically but are never a major source of food, as are placentae of elephant seals (*Mirounga leonina*) at Heard Island (Downes and others, 1959) or those of Weddell seals (*Leptonychotes weddelli*) at the Windmill Islands (Eklund, 1961). The Weddell seals breed at Signy Island before the skuas arrive and the breeding population of elephant seals is too small to be important. Kitchen refuse provided a continuous source of food, and before egg-laying many skuas foraged around the station, but, for some unknown reason, only those with territories adjacent to the station and non-breeders fed there later.

Counts were made of the remains of petrels at nests in the study area throughout one breeding season. Only remains of those species nesting within a territory were found in it. The total number of remains found in any territory indicated that no pairs used petrels as a major supply of food. Remains were found throughout the breeding season but only in quantity from the last week of December to the last week of January, for no apparent reason, and when the juvenile petrels started to fly. The latter was the only time that cape pigeon remains were common. The only species of bird on Signy Island for which there are no records of predation by skuas are the blue-eyed shag and the sheathbill (*Chionis alba*).

Reactions to skuas. Wilson's petrels and dove prions have been seen avoiding pursuing skuas by jinking. The following species have been seen mobbing skuas: giant petrel, Wilson's petrel, dove prion, snow petrel and the Antarctic tern. In mobbing, one or two birds simply fly behind a skua but the Antarctic terns swoop and soar over standing skuas, causing the latter to bob the head as the terns pass. I have also seen flocks of about 50 terns chasing a skua. In view of the relative immunity of the cape pigeon, it is of interest that this is the only species of petrel on Signy Island that I never observed mobbing skuas. Cape pigeons also seem to be unique in the defensive reaction of holding out the carpal joints and spreading the tail, as illustrated by Pinder (1966). This reaction is often directed at humans coming near a sitting cape pigeon, and I have observed swimming juveniles reacting this way to skuas hovering low overhead. While these cape pigeons were not attacked, it is not possible to say whether it was the reaction that deterred the skuas.

Conclusions

The relatively small breeding population at Signy Island and the part-time nature of the study have allowed little more than qualitative description of the breeding biology of *C. s. lönnbergi*.

The Signy Island population has been shown to differ from other populations studied in high breeding success, low nest density and late age at first breeding. It is unlikely that these result from taxonomic differences between the different subspecies involved, but more to differences resulting from the environment in which each population lives. There are, in fact, similar differences between populations of the same subspecies, for example, *C. s. maccormicki* at Cape Royds and Cape Hallett. Other differences that have been noted, such as the absence of a call by the adults before feeding the young, may be due to sparsity of observations and therefore might not be real.

There is no evidence that colonization of Signy Island by skuas was recent or that the

population was much smaller in the 20 years prior to the first census in 1958, so the increase in the breeding population noted since 1958 seems to be a recent change of a formerly fairly stable population. In view of the apparently favourable conditions, it is surprising that the breeding population is so low. Furthermore, there does not appear to be a shortage of food during the breeding season that would limit the output of young. On the present data, it is impossible to gain any idea of the extent of mortality occurring between fledging and first breeding.

It is difficult to explain why nests should be so well spaced at Signy Island, especially since nests are much closer in other areas. Predation by skuas on one another's young would be less with distant nests than with close ones, and at Signy Island there seems to be no counteracting pressures for nesting closely, such as limited terrain or localized food sources. However, on the basis of this study, it is not possible to say whether reduced predation by skuas on one another's young at Signy Island is due to abundance of alternative food supplies or to the nests being well-spaced.

ACKNOWLEDGEMENTS

This work would have been impossible without the help of my companions on Signy Island and the keenness of my predecessors, notably N. V. Jones, R. Pinder, P. A. Richards and F. W. Topliffe, who made valuable observations and carried out banding work prior to my arrival.

Dr. D. L. Lack very kindly allowed me to use the facilities of the Edward Grey Institute of Field Ornithology, Oxford, while writing this paper. During this stage I was encouraged and assisted by Dr. I. Newton.

Finally, I am grateful to Dr. M. W. Holdgate and Mr. E. A. Smith for continued help and encouragement.

MS. received 1 April 1967

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