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THE BROWN SKUA
Catharacta skua lönnerbergi (Mathews)
OF SOUTH GEORGIA

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far been published; it is hoped that these notes may serve as a basis for future studies and for comparisons with closely related species.

Brown Skuas are plentiful on South Georgia, breeding generally within two hundred metres of the sea and seldom far from others of the same species. First appearing in August or September (and usually from the east) they settle in small groups about the coast and adopt territorial behaviour almost immediately. Flocks of unpaired birds, however, persist throughout the breeding season and are usually to be found where food is abundant. The breeding season extends from October to March, after which the birds leave the island until the following spring. Lönnberg (1906, 58) reported seeing large numbers of skuas at sea north of 47° South before mid-October but very little else is known of their distribution and movements away from the breeding grounds. It is possible that the whaling and sealing industries of South Georgia have helped to maintain larger populations of skuas, particularly in juvenile stages, than the island would otherwise have supported.

b. Taxonomics

The species *Catharacta skua* (Brünnich) includes three well defined subspecies and a fourth which may require further subdivision. The three distinct forms are:

Catharacta skua skua (Brünnich). The Great Skua of the North Atlantic Ocean.

Catharacta skua chilensis (Bonaparte). The Chilean Skua of South America.

Catharacta skua maccormicki (Saunders). The McCormick Skua of the Antarctic coastline and off-lying islands.

The fourth group have been called collectively Sub-Antarctic or Brown Skuas, the latter name distinguishing them from the chestnut Chilean and grey McCormick Skuas with which they share the Southern Ocean. They are found on all the sub-Antarctic and temperate islands of the South Atlantic Ocean as far north as southern Australia. Throughout their extensive range they are similar in way of life and appearance, but attempts have been made to divide them into races or subspecies on the grounds of their geographical distribution, measurements, or plumage colouring. Lowe and Kinnear (1930, p. 113) and Peters (1934, p. 309) accepted four subspecies

Catharacta skua antarctica (Lesson) of the Falkland Islands, Tristan da Cunha and Gough Island.

Catharacta skua clarkei (Mathews) of the South Shetlands, the South Orkneys and South Georgia.

Catharacta skua intercedens (Mathews) of Kerguelen and the Crozets, and

Catharacta skua lönnbergi (Mathews) of New Zealand and associated islands.

Hamilton (1934) concluded, from examination and measurement of skins in the British and Royal Scottish Museum collections, that only two subspecies could reasonably be maintained on grounds of measurement, and he grouped the birds as follows:

Catharacta skua antarctica (Lesson), of the Falkland Islands and South Shetland, and

Catharacta skua lönnbergi (Mathews), of New Zealand, the Crozets, Kerguelen, South Georgia, the South Orkneys, Tristan da Cunha, Gough Island and the South Shetlands.

Hamilton drew attention to the faded condition of most of the skins which he examined, and concluded that plumage differences could not be regarded as valid subspecific characters. It would seem, however, that more descriptions of skins, unfaded or in similar conditions of fading, are required before the value of colour variation as a taxonomic character can properly be assessed. On their return to the breeding grounds in August and September the South Georgia birds' colouring is rich chocolate-brown; within a few days fading becomes apparent and by the end of September the birds are grey-brown with pale mottled neck and chest and darker underparts, wing coverts, and quills. This colouring is retained throughout the remainder of the breeding season: later the birds are readily distinguishable from their newly fledged chicks which retain their darker colour with little fading until they migrate late in autumn. The intense and highly actinic light, enhanced by reflection from the snow-covered ground in spring, may account for earlier fading in adults. No adult in unfaded plumage was examined closely as the birds were difficult to approach during the first few days after their return. Newly fledged chicks were, however, found to have a markedly chestnut-coloured fleck on the tip of each mantle and collar feather, giving them a distinct chestnut or mahogany brown tinge in sunlight. This faded quickly and the chicks assumed a darker chocolate-brown hue similar at a distance to that of a newly returned adult. So far as I am aware no

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Section I

BROWN SKUAS AND THEIR ENVIRONMENT

a. Introduction

FROM October 1953 to January 1955 the author was engaged in a study of King Penguins (*Aptenodytes patagonica* Gray) on the island of South Georgia. A base hut was established at the Bay of Isles (54°04' S., 37°24' W.), and daily observations were maintained throughout two breeding seasons and a winter. Opportunities were presented for the incidental study of other species, and this report describes the activities of a population of Brown Skuas which occupied the locality during the breeding seasons. Seven pairs of skuas nested in the first season and nine in the second; all the breeding birds and their offspring were marked with coloured and aluminium leg bands, and many non-breeding birds which visited the area from time to time were also marked. Incubation had started in some of the pairs when observations began in 1953, but pairing and courtship were witnessed in the following spring. Although Brown Skuas have attracted the attention of most visitors to South Atlantic islands very few details of their behaviour have so

species of birds most of which depend directly on the sea for a living. The north-eastern side of the island is more densely populated than the colder southern side.

The Bay of Isles is an extensive bay toward the north-western end of the island. Three large glaciers terminating in ice cliffs, steep rock faces and occasional small beaches line the bay, which is protected to a limited extent from northerly swells by the arm of Cape Buller (see Fig. 1). The locality studied is part of the raised beach system which can be traced at various points along the coastline on the north side of South Georgia; here it has an average width of 100 metres and is limited on the landward side by an old sea cliff 15 to 30 metres high (Plate 1a). From the foot of the cliff a belt of tussock grass extends across rather more than half the width of the beach. Scree slopes, and all but the steepest faces of the cliff, are covered with a luxuriant growth of mosses, lichens, and grasses; behind the cliff lies a ridge of rolling grassland rising at the western end to 200 metres. Inland from the ridge is a basin of barren glacial moraine uncovered by recent retreats of Grace Glacier. The area contains a rookery of about 5000 King Penguins and two diffuse breeding groups of Gentoo Penguins (*Pygoscelis papua* Forster); it is, in addition, the breeding ground for over a hundred elephant seals (*Mirounga leonina* Linn.).

The locality is similar in most respects to many other stretches of shore along the northern and eastern sides of the island. Each section bears its population of Brown Skuas, usually but not always associated with penguin rookeries. Breeding pairs are also found on off-lying islets, where they associate with Terns (*Sterna vittata georgiae* Reichenow), Giant Petrels (*Macronectes giganteus* Gmel.) and Wandering Albatross (*Diomedea exulans* Linn.). Breeding pairs occupy large territories, and areas which, for one reason or another, are unsuitable for territories are used by groups of non-breeding birds for sleeping and standing about. Non-breeding birds are found in large numbers about the whaling stations during the whaling season, and are invariably present whenever seals are killed along the beaches. Pintado Petrels (*Daption capensis* Linn.) also attend the sealers' activities; unlike the skuas these seem to follow the sealing vessels in their travels up and down the coast.

From April to October the beaches and cliff tops are permanently snow-covered, the snow level rising gradually during the winter until the nesting sites are buried three to four feet deep. The thaw is usually rapid, and for the remainder of the year the sites are clear of snow except for transient coverings during short spells of cold and snowy weather. The climate experienced during the period of observations is summarised in Table I. In general the weather was cold, windy and wet, with frequent drizzle from overcast skies and occasional heavy rain in the summer. The heaviest rains and strongest winds were associated with northerly upper-air circulation and were usually warm; the clearer skies associated with southerly weather could give rise to sharp evening ground-frosts at any time during the summer, and only in February and March was the ground sufficiently warmed during a sunny day to maintain temperatures above freezing point throughout the night.

Month starting	Mean Daily	Mean Max.	Mean Min.	Extreme Min.	Mean Wind (Kts.)	Precipitation (mm.)
1.12.53	39	43	35	27	7	174
29.12.53	39	43	35	30	9	119
26. 1.54	41	45	37	30	7	143
23. 2.54	38	41	35	30	10	195
23. 3.54	39	43	35	25	11	198
29. 4.54	36	40	33	23	9	181
18. 5.54	30	33	26	18	10	167
15. 6.54	32	35	29	16	12	154
13. 7.54	28	30	24	12	11	131
10. 8.54	27	30	24	6	11	213
7. 9.54	29	32	26	11	14	146
5.10.54	34	37	31	22	9	90
2.11.54	38	43	35	29	9	74

TABLE I. Summary of climate at the base, Bay of Isles, December 1953 to November 1954.
All temperatures in °F.

d. *Methods of Study*

Brown Skuas presented themselves for study from the moment when the first load of stores was sent ashore. The pair in whose territory the hut was built were the first to be noted; they watched closely, removed all small and portable objects, stole sandwiches and left the building site only to chase off other intruders. By contrast, three pairs of Black Backed Gulls (*Larus dominicanus* Licht.) nesting 100 metres from the site abandoned their eggs within two days of the party's arrival. All the skuas soon lost the little timidity which they at first possessed; a pair not otherwise engaged would accompany the observer as he moved within its limits, leaving him at the territory boundary to be escorted by the next pair. Boundaries could in this way be ascertained clearly, and the territory significant to a pair could be defined as that area within which the birds were prepared to escort the observer.

The birds' curiosity made it possible for them to be trapped without difficulty for ringing and weighing: a string loop on the ground with a pair of gloves for bait was sufficient to catch any of the breeding birds. As some confidence was lost for a short time after handling, they were trapped only for ringing early in the season and very occasionally for weighing later. Wandering birds could be trapped at any time by laying the loop alongside the seal carcass from which they were feeding. Later it was found that incubating birds could be lifted off the nest and ringed while resting on the observer's outstretched hand. This method occasioned no alarm and was much to be preferred. Each marked bird carried one aluminium ring supplied by "Discovery" Investigations, bearing a four-figure number and instructions for informing the British Museum (Natural History) if recovered. In addition, the breeding birds bore coloured celluloid rings, as used for poultry marking. Of the celluloid rings the spiral type was found to be more durable than the wrap-over type; only the pink rings were of the latter kind and these were missing when the birds returned from migration. An account of rings used appears in Stonehouse (1956); Table II in this report shows the ring numbers of all breeding birds and chicks.

Bird	Probable sex	"Discovery" Ring
Yellow-Green Left	♂	4884
Yellow-Green Right	♀	4883
Green Left	♀	4859
Green Right	♂	4858
Yellow Left	♂	4852
Yellow Right	♀	4853
Pink Left	♂	4854
Pink Right	♀	4860
Mauve Left	---	4871
Mauve Right	---	4881
Mauve-Green Left	♀	4889
Mauve-Green Right	♂	4870
Yellow-Mauve Left	♀	4885
Yellow-Mauve Right	♂	4886
Silver Left	♂	4914
Silver Right	♀	4915
Mauve-Silver Left	---	4898
Mauve-Silver Right	---	4899
Mauve Chick	---	4880
Green Chick (1953)	---	4857
Mauve-Green Chick (1953)	---	4888
Yellow-Mauve Chick (1953)	---	4887

TABLE II. Permanent markings and probable sex of breeding birds and chicks.

Individual birds are identified according to their coloured rings. Thus Mauve-Silver Right bore both mauve and silver bands on its right leg; its partner Mauve-Silver Left bore both on the left leg and the two formed the Mauve-Silver Pair*. Chicks were marked with their parents' colours on both legs where two colours were involved, or with two bands of the same colour on one leg where only one colour was used.

* The colour combinations are not intended to suggest affinities with other pairs bearing either colour singly or combined.

The birds were easy to photograph in most of their activities, settling back to normal behaviour within a few minutes of my arrival. A hide was in one case erected near to a nest site in an attempt to secure photographs of nest-building, but it was never possible to enter the hide without the full knowledge of the birds, who would sit patiently outside, occasionally peering in through the flap to see what I was doing. The presence of the hide seemed to exercise their curiosity more than the undisguised presence of the observer. This confidence and interest was perhaps based on the fact that in the previous season they had been "trained" to fly up and receive food whenever the territory was visited, so that the identity of the incubating bird could be noted without actually visiting the nest.

Eggs were measured, using calipers on a steel rule, and weighed on the tray of a spring balance graduated to 1 kg. in divisions of ten grams. This latter instrument, selected for weighing penguin chicks, was unsatisfactory for skua eggs as all the weights were about 100 grams and the balance was insufficiently accurate to record small differences faithfully; no materials were at hand to make a more accurate balance about this range. Four of the first season's chicks were weighed and measured periodically, using the same apparatus with the addition of a larger balance graduated to 20 kgs. in 100 gram divisions. This too left much to be desired as a means of weighing birds of between 1 and 2 kgs. weight; it was also used to weigh adult birds, whose weights fell within the same range. Both chicks and adults were suspended in cotton bags for weighing. Egg dimensions and weights appear in Table III, and the weights of four chicks appear in Table V. Fourteen adults, weighed between December 1953 and March 1954, averaged 1.8 kgs., spread between 1.2 and 2.1 kgs.

BREEDING SUMMARY, 1953-54

Pair	Egg	Wt. (gms.)	Length (cms.)	Diameter (cms.)	Laid	Hatched	Fate
Yellow-Green	1	100	7.3	5.2	—	—	Removed 26.11
	2	100	7.3	5.3	—	—	Failed to hatch
Green	1	90	7.3	5.3	15.11	17.12	Successful
Yellow	1	100	8.0	5.3	*2.11	4.12	Killed 7.12
	2	105	8.0	5.3	*3.11	5.12	Disappeared 10.12
Pink	1	115	8.2	5.1	—	—	Lost in incubation
	2	120	7.9	5.3	—	—	Lost in incubation
Mauve	1	115	7.7	5.8	—	—	Removed 26.11
	2	120	7.9	5.8	*31.10	2.12	Successful

* Estimated

Mauve-Green and Yellow-Mauve pairs each raised one chick

BREEDING SUMMARY, 1954-55

Pair	Egg	Wt. (gms.)	Length (cms.)	Diameter (cms.)	Laid	Hatched	Fate
Yellow-Green	1	100	7.3	5.2	20.11	—	Successful
	2	105	7.3	5.1	23.11	—	Removed
Green and Yellow	1	95	7.1	5.1	25.11	—	} One successful
	2	100	7.1	5.1	27.11	—	
Pink	1	105	7.8	5.5	*13.11	15.12	Successful
	2	100	7.4	5.1	*16.11	—	Removed
Mauve-Green	1	100	7.3	5.5	14.11	16.12	Successful
Yellow-Mauve	1	120	7.7	5.6	25.11	—	Broken
	2	120	7.8	5.5	28.11	—	Successful
Mauve-Silver	1	105	7.4	5.1	22.11	—	Successful
Silver	1	100	7.2	5.2	29.11	—	Successful

* Estimated

Mauve pair failed to breed

TABLE III Summary of Egg Dimensions and Breeding Success, 1953-55.

Skin temperatures were measured using a variable resistance ("Thermistor") probe coupled to a Wheatstone Bridge circuit; for a discussion of similar and more complex forms of this apparatus see Mortimer and Moore (1953). Skin, cavity and egg temperatures are recorded in Table IV.

Embryos from cracked eggs and dead chicks were preserved, but no skins or anatomical specimens were taken. It was therefore not possible to determine the sexes of breeding birds with certainty. At the time of egg-laying the bird which retired to the nest area and seldom appeared elsewhere in the territory was usually more bulky in appearance than its mate; this bird was in the lower position in copulation and was assumed in all cases to be the female. However, as all observations on skuas were necessarily incidental to other work, it was never possible to watch behaviour for long, and behaviour accounts in this report are not in general sufficiently complete for a knowledge of the sex of the bird to be critically important. The probable sex of most of the breeding birds is indicated in Table II.

Bird	Skin Temperature	Cavity Temperature	Egg Temperature
Green Right	102-103	101	—
Yellow Right	103	101	Upper surface 101 Lower surface 96
Mauve Left	103	101	Interior 96
Yellow-Green Right	102-103	100-101	Interior 96

TABLE IV. Skin, cavity and egg temperatures in four incubating birds, 26th November, 1953. Air Temperature 47-50. All temperatures in degrees Fahrenheit.

Section 2

BEHAVIOUR

a. General Characters

MURPHY's account of the species (1936, p. 1025) is an entertaining description of an impressive and lively bird. "During the South Georgia Expedition of 1912-3", he writes, "I became extremely well acquainted with the Brown Skua, which has left, I believe, a more vivid impression in my memory than any other bird I have met. The skuas look and act like miniature eagles. They fear nothing, never seek to avoid being conspicuous, and, by every token of behaviour, they are Lords of the far South". The key to their character may perhaps be found in Murphy's description of them as "... gulls which have turned into hawks". Their remarkable curved talons, aerial agility, advantage in size and power, and capacity for individual behaviour fit them well for their life of predation, scavenging, and piracy; on the occasions when they compete against Black Backed Gulls for food or nesting space, it is the gulls which inevitably find themselves at both physical and mental disadvantage. Only Giant Petrels can oust the skuas from a feeding site.

The Brown Skua is in no sense a colonial bird. Traces of colonial behaviour may perhaps be seen in the close proximity of four nests at adjacent corners of their respective territories in the first season; in all other respects the birds are solitary in their breeding behaviour, and sociable when not breeding. Suitable stretches of ground are parcelled out between them, territories are extensive, and much energy is devoted to expelling intruders once the claims have been established. Unoccupied (i.e. non-breeding) birds congregate on neutral ground, feeding communally but showing little of the concerted action which may be seen in similarly disposed groups of gulls. The groups are dominated by one or two birds to which all others are submissive; quarrels are frequent but short-lived, and no injured birds were seen.

Although they may in general terms be called sea birds, Brown Skuas are seldom seen to have any direct dealings with the sea at all. Little is known of their behaviour during the southern winter, when presumably much of their time is spent at sea. Once at South Georgia they become land birds almost exclusively, in fact only on one occasion during the two seasons' observations was a bird seen to settle on the open water. They wash in freshwater pools and streams, and take food from the shore, from other species of birds, or from each other, but seldom directly from the sea itself. In the air they are graceful and efficient, capable of sustained climbing flights and rapid changes of speed and direction. In spite of their greater weight they can

overtake and outfly Black Backed Gulls with ease. They are adept at catching morsels of food in mid-air, and are capable of controlling their flight to an unusual degree in strong, gusty winds. It became the habit of Yellow-Green Left, one of the more frequently visited birds in whose territory the base hut was established, to accompany me in walks along the cliff top where the pair's nest was to be found. On windy days, with steady winds of twenty knots and gusts of up to twice that speed, Yellow-Green Left would station itself one metre above and slightly behind me, keeping station with wings motionless and wide-spread, and making only small compensating movements with tail, head and wings to allow for variations in the airflow. On still days flight was more difficult and all the birds preferred walking; Yellow-Green Left would patter along behind the observer in tours of the territory, fluttering occasionally to keep up if the pace were excessive and breaking into agitated flight only if the nest were approached too closely. Similarly the Green pair would follow through the tussock grass at a distance of three or four metres. On one occasion I was obliged to search the whole of the beach tussock patch in Green territory for a spring balance which had been carried off and dropped by one of the birds. The search took three hours, and during the whole time the two owners of the territory trotted patiently behind. Flying over short distances clearly involved an effort which they were not prepared to make, and birds would frequently spend a whole afternoon walking quietly about their stretch of beach or rookery, turning over stones, examining old bones, and, on days of calm seas, paddling in the edge of the water.

The tall tussock grass on the upper half of the beach was generally avoided; here the grass clumps rose to a metre and more in height. Penguin paths winding between them and seal wallows or small pools in the badly-drained areas apparently did not attract the birds. Occasionally, wandering skuas were forced down into them and beaten by the enraged owners, and the fledgling chicks walked through in their exploration of the territories. Although providing cover from aerial attack, the tussock-covered beach areas were generally useless to the birds.

b. Aggression, Submission and Defence

Enemies on the ground could be combated in either of two ways. Man, and large birds or trespassing skuas, were generally made the subject of vicious diving attacks; the offended pair would swoop in long arcs starting and ending thirty metres in the air, coming in at the target from different directions. At low intensity the birds would miss the target by one or two metres; as the attack increased in intensity each swooping bird would lower its leathery feet on passing over and hit the offender resoundingly. The performance was usually accompanied by alarm calls, high pitched, intermittent, raucous screams as the birds were rising and turning to make their next run. Skuas on the ground responded to these attacks by crouching low with head and neck extended along the ground, rising as the attacker passed over to give a full-throated challenge call with raised wings, and crouching again at the next swoop. Between skuas, these attacks were seen most frequently in boundary disputes, when the defenders had spotted trespassers from the roost. Flying straight in, they could very occasionally take trespassers by surprise, bowling them over at the first run and then chasing them in a running aerial fight when they had picked themselves up and flown off. Frequently the defending pair would carry the battle into the neighbours' territory, swooping over an incubating bird or over the trespasser when it had returned to its roost.

Disputes over food were usually settled by threat display on the ground. They were seen in breeding birds before pairing and after the pairs had split, and in the non-breeders at any time of the year. Dominant birds approached those whom they challenged with a "challenge-walk", an erect attitude with neck held vertically, collar feathers fluffed out, and wings held slightly out from the cover of the mantle. Occasionally the neck would be bent sideways away from the victim as the aggressor stalked deliberately past. If inclined to hold its ground the challenged bird would adopt the same attitude and the two might encircle each other for some minutes before one or the other became submissive. Submission was indicated either by rapid walking off and flight, perhaps with the aggressor in pursuit, or more frequently by the loser settling on the ground and digging the tip of its beak repeatedly into the surface with lateral movements of the head. If originally standing by food the loser would gradually be forced away, keeping a distance of about a metre between itself and the aggressor; an agitated chattering call was often heard from the weaker bird, while the aggressor gave a series of louder intermittent yells which frequently culminated in the full "challenge display" (see below). Fights could develop from such threat displays; one or other bird would throw itself into the air with wings partially extended and feet thrust forward; hooked talons were used for gripping, but were more often seen to be lashing back and forth as two birds fought with interlocked beaks.

A more active and widely used show of aggression was the "challenge display", seen in a variety of circumstances where ownership, temporary or permanent, was involved. The displaying bird would extend its wings obliquely upward and back, showing to full advantage the white bars on the under-surface (Plate Ib). With body erect, chest out and beak wide, a series of full-throated yells would be given in accompaniment to the visual effects. This display was the one most frequently seen, being given on landing in their territory, on seeing other skuas passing overhead, between attacks from other skuas, and between rounds of pitched battles fought with other skuas over carcasses. It also appeared when the owner had landed alongside a trespasser in its territory, usually to the discomfort of the intruder, and could be evoked artificially at any time by allowing an owner to see itself in a mirror. Members of a pair displayed together, the two birds being affected equally by the same stimuli. A slightly less intense version of this display was seen when the displaying bird was at the same time in some fear of the bird at which it was displaying. Thus the Green pair, who were dominated by their more aggressive Yellow neighbours in the first season, would display loudly if the Yellows landed in the amphitheatre near to their nest, but with beaks tucked into their ventral neck feathers in an almost vertical position, their calls gradually dying in volume as the Yellows themselves shrieked in unison.

Boundary disputes were frequently settled by a specialised display, a version of the challenge-walk, which alternated with the raucous and impressive challenge display. It could be evoked by placing an egg or other bait on the boundary in the small amphitheatre, mentioned above, when both pairs were present. The boundary itself was a small stream, but about two metres of ground on either side were neutral territory not to be entered in the presence of the neighbours. Both pairs would parade up and down their respective sides of the neutral ground, challenging occasionally but frequently bobbing their heads low, with beaks pointing to the ground or slightly back between their legs. This action would be accompanied by a slow intermittent call with beak slightly opened, the call almost stifled in the bird's throat. After a few minutes of such behaviour one bird, closely followed by its mate, would gradually move forward in the same attitude while the others retreated. Approaching the egg, the winners would continue their display until alongside. Then the spell would be broken, the egg snatched, and the successful pair would fly back to their own ground to the accompaniment of the challenge calls of their rivals. This display was intense in performance and seen only in circumstances where both parties held equal claims, i.e. on a territory boundary. With the two pairs mentioned, the Yellows were invariably the ones to advance; sometimes they would be successful in securing, by the same means, an egg placed two or three metres within the Greens' territory. However, the Green nest site was not far from the boundary at this point and the nest area was always guarded with more certainty than any other part of the territory. Greens advanced into Yellow territory only in the absence of one or both Yellow birds.

Incubating birds responded to approaching danger by uttering repeated, warbling, plaintive alarm calls; these invariably brought the partner up to the nest site if it were within earshot. The calls increased in frequency and intensity as the intruder approached, and ended with the bird flying straight off the nest and into attack. Simultaneously, the note changed to an aggressive scream. The nest alarm call was always used when the observer approached the nest but was never heard as a challenge to birds flying overhead. If the observer stayed in the area the calls would die away to quacks, delivered antiphonally as the birds stalked uneasily around; any sudden movement would be greeted with renewed alarm calls. During the "uneasy" stage, birds frequently settled facing the observer, sometimes to pull violently at moss or grass immediately in front of them, a perfect example of a "displacement activity" as described in Herring Gulls and related species (Tinbergen, 1951, p. 115, and 1955a, p. 65). A similar display was seen on one occasion when a Giant Petrel, grounded by calm weather, blundered into Green territory and came to rest below the cliff three or four metres from the nest. After swooping had failed to dislodge it, Green Left incubated, calling intermittently, while Green Right sat midway between nest and intruder tearing up the turf energetically.

The low-pitched quack was heard in circumstances of low intensity alarm. When any bird, having challenged its own image in a mirror placed in its territory, attempted to search for the intruder in the area behind the mirror, the search was invariably accompanied by gentle quacks. Birds handled on the nest quacked, and sometimes pecked very gently at the observer's clothing or fingers but never so violently as when handled elsewhere in the territory.

In general Brown Skuas are silent birds, seldom calling on the wing and shrieking only when defending their property. Their calls, however, are remarkable for their volume and persistency; when necessary, they can be maintained with ear-splitting force for twenty minutes without pause.

c. Feeding Behaviour

Brown Skuas are catholic in their tastes and inclined toward experiment. As their gullets seem to operate with equal facility in either direction, the swallowing of indigestible material along with more orthodox foods causes them no inconvenience; more than one bar of soap, a quantity of material impregnated with formalin, corks, and alcohol-soaked cotton-wool were missed from the work table by the hut, to be recovered later in pellet form not far from the Yellow-Green nest. It was necessary to extinguish cigarette-ends before dropping them in the presence of a skua; any small object found on the ground would be picked up immediately, and usually swallowed forthwith. The consistency of the material seemed important; in general small hard objects were rolled about or pecked hard once they had been held in the beak, softer objects of convenient size were swallowed whole. Smooth, rounded objects were treated as eggs; if small they were carried away, if larger they were dealt with on the spot, the bird standing over them squarely and attempting to pierce the surface by well directed blows from above with the tip of the beak. The shoulders of Kilner jars were subjected to this treatment, as were the sides of tins and small bottles and disused radio valves. This method of egg opening was apparently unknown to fledgling chicks, who were unable to deal with Gentoo or King Penguin eggs until the parents had opened them. Rats, which formed a very small proportion of the diet, were crushed by the beak before being torn in half and swallowed. Unwieldy masses of food could be swallowed and regurgitated several times before finally being digested; both chicks and adults disgorged food when agitated, returning to swallow it again when the alarm had passed.

Larger objects were torn to pieces: seal steaks three to four kilos in weight could be torn by holding and shaking. The feet were never used to hold down the material which was being torn by the beak; this point was watched for carefully on many occasions, in view of conflicting evidence from Buller (1888, 63) and others and of the author's own observations on McCormick Skuas in which such an action was never seen. Paired birds, and occasionally unmated birds tolerating each other's presence at a feeding site, tore material between them, each holding an end and tugging hard against each other with feet braced (Plate IId). Paired birds feeding in these circumstances shared the torn morsels equally.

These methods of dealing with a variety of materials were well adapted to the types of food which constituted the skuas' normal diet. Stillborn and crushed seal pups, carcasses of penguins and seals, and Gentoo and King Penguin eggs and chicks formed the bulk of the diet in the vicinity of the base hut; there were no signs of predation on other species of birds and the mobbing of other birds, forcing them to drop or disgorge food, was seen on very few occasions. During August and September there was little for them to feed on at all. In September 1954, when the first birds returned from migration, most of them fed at the King Penguin rookery, on the carcasses of long-dead chicks. On 21st September, a visit from the sealers provided four carcasses which drew forty-five skuas to the beach. The rookery was closed to wandering skuas once the Pink pair had returned to defend it (23rd September), and throughout October most of the feeding observed was on seal birth-membranes, dead pups, and the carcasses which the sealers occasionally supplied. The first Gentoo eggs were laid on about 8th November, and from then onwards those pairs with Gentoo nests in their territories were able to feed at will. Eggs carelessly incubated or abandoned for a moment were snatched immediately by skuas watching from high rocks above the Gentoo nests. Such birds swooped down when opportunity offered, grasped the egg in the beak and flew to safety. Eggs offered to skuas away from the rookery were recognised at once and were usually carried some distance before being opened.

Gentoo chicks were removed from the nests exactly as were the eggs; later, when they had left their nests and joined crèches, odd chicks were killed when momentarily isolated or sleeping away from the crowd. Such chicks were torn open and their viscera and crop contents were removed completely. Those pairs of skuas which did not have Gentoo nests in their territories were still able to bring krill (which had presumably been fed by parent Gentoos to their chicks) to their own chicks, while the seal carcasses remained almost untouched by the breeding skuas. Later in the year when the newly fledged juveniles gathered with the non-breeding birds, seal carcasses were again consumed by the breeders; the Gentoo chicks were at this time too big to be attacked. There was no apparent shortage of food at the time when the breeding birds were disappearing on their migratory flights.

A few rats were taken; these, the descendants of ships' rats brought to South Georgia by the sealers, are strictly nocturnal in habits, and on moonlit nights the skuas could often be seen flying low over their runs. Another intermittent source of food was the plankton; on occasions when persistent northerly winds blew

the surface waters toward the beach, a thick deposit of copepods and small amphipods would be found at high water mark. This the skuas scooped up, ignoring, however, the equally plentiful supply in the water itself. On these occasions shoals of Pintado Petrels fed inshore, some hundreds of thousands being seen in the bay at once; these, in contrast, fed only in the water and equally firmly ignored the deposits left by the lapping waves on the sand. Floating debris washed ashore after heavy ground swells was picked over carefully by the skuas, but the rock pools and alga-covered rocks at the western end of the beach were left for the gulls and sheathbills (*Chionis alba* Gmel.).

d. Territory

In October 1953, the area between Grace Glacier and Markham Point was found to be divided into seven territories, each occupied by a pair of skuas and each, sooner or later, containing a nest with one or two eggs. Fig. 2 shows the territory boundaries and nest sites. Boundaries usually coincided with natural and easily recognisable landmarks such as the edge of a cliff, a stream, or the side of a pond, in the tussock grass or on the shingle of the beach where no such natural landmarks existed, the boundaries were apparently real and recognisable by both pairs; they usually lay at right angles to the line of the beach and continued the direction of a jutting section of cliff. Not all sections of boundary were patrolled or defended with equal vigour; each territory contained one or more roosting sites from which most of the ground could be surveyed; the roosts generally overlooked those parts in which trespassing was most likely. Thus, as wandering birds were most likely to be found about the shore and among Gentoo nests, roosts were chosen which overlooked and gave easy access to those areas. Boundaries visible from the roosts were carefully watched and guarded, others were defended only on rare occasions and, where no natural marker existed, were in many cases indeterminate. Boundaries extended down to the sea and no further, and any bird was permitted to fly along the coast so long as it remained over the water.

Pairs seldom quarrelled over territory boundaries, which seemed to be well recognised from the outset. A quarrel could be induced experimentally at any time by luring a bird into its neighbours' territory on the visual promise of food, e.g. a penguin egg. Normally inquisitive and alert up to the boundary, the intruder would cower, become furtive and watchful toward its neighbours' roosting site, move rapidly up to the bait and, if undisturbed, would drag it over the border into its own ground or gobble it quickly on the spot and run back. Their apprehension was apparently directed only toward the territory owners, whom they appeared to recognise. In an experiment with a mirror Green Right, poaching in Yellow-Green territory, suddenly saw its own reflection; it dropped its food and gave a challenge display at the reflection, approached it in a threatening attitude and finally attacked it. The Yellow-Greens were absent at the time, but shortly afterwards Yellow-Green Left flew in, challenged with a call from a knoll five metres away, and Green Right fled from the scene. Pairs usually spotted any intrusion into the surveyed parts of their territories and swooped immediately and successfully; normally, if both were unoccupied, they defended their ground together, but a single paired bird very seldom had difficulty in driving off an intruding pair except in special cases in which food was placed actually on the boundary line. After swooping, the defender would settle by the boundary and, with wings extended, give a full antagonistic display with challenge calls, to which the neighbours would similarly reply. Swooping was effective as a threat and also as an actual attack. Generally, however, settled pairs seldom had occasion to antagonise their neighbours by visiting the boundaries at all. Although the boundaries were clearly defined when the need for definition arose, they were visited only infrequently and disputes were therefore rare. Skuas from neighbouring nests seldom took off over each others' territories whatever the direction of the wind.

Skuas flying over the territories were always challenged by owners. Gulls were usually chased, particularly if the territory owner happened to be in the air at the time of the intrusion. Giant Petrels seldom earned more than an upward glance, and the minute South Georgia Pipit (*Anthus antarcticus* Cab.) was ignored completely. The challenge call and display was seldom used against any bird other than a skua.

Territories varied considerably in size; approximate areas defended in both seasons are shown in Figs. 2 and 3. The amount and quality of feeding possible in each territory was also variable. Those which included a stretch of beach conferred on their owners rights over any edible material washed up (e.g. heavy swarms of plankton washed in by onshore winds), and over debris left by seals (placentae, membranes, dead pups). Territories which included penguin rookeries were of considerable value once the penguins had started to breed, for the skuas were apparently able to secure Gentoo eggs and small chicks whenever they made the effort. They also had a constant, though less assured, supply of abandoned eggs and chick corpses

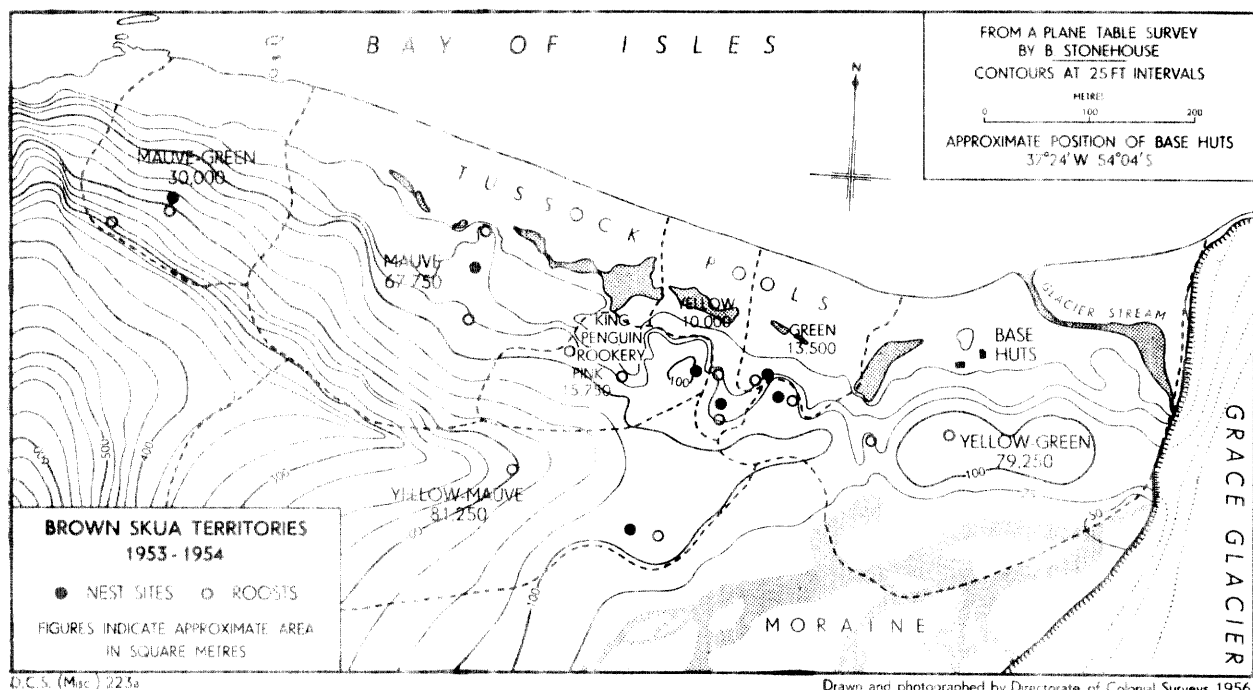


FIGURE 2. Brown Skua territories, 1953-1954.

from the King Penguin rookery. Rights over these food sources were rigorously guarded and very little poaching was seen. However, it is clear that other sources of food were available outside the territories. On more than one occasion a bird was seen to take off from its roost, circle high over its territory, and fly off out of sight along the coast, returning one or two hours later to deposit a cropful of krill (no doubt removed from the crop of a Gentoo chick) at the feet of its chick. It is possible that hunting for food of this nature would be easier in rookeries larger than the local Gentoo rookeries; few strangers were seen to visit the carefully defended and perhaps relatively small, local rookeries. The possibility that the krill was collected directly from the sea cannot altogether be excluded, but it seems extremely unlikely in view of the general nature and feeding habits of the birds.

Occasionally, however, wandering birds were seen to settle in overwhelmingly large numbers in a territory which temporarily contained a considerable bulk of food. Thus, during November and December, whenever the sealers visited the area leaving up to half a dozen flensed carcasses on the beach, or whenever a seal was shot for dissection, large numbers of skuas would fly in to feed on the remains. The owners of the territory, quite unable to deal with so many interlopers, would soon become indistinguishable from the rest, feeding and fighting alternately, then retiring to their roost to watch and returning only to drive away the last few from the cleaned bones. Among the intruders would occasionally be seen one or more neighbours, no doubt attracted by the sight of others feeding. It is suspected that these flocks of intruders were in general non-breeding birds without territory. Many were ringed, and were later seen on Salisbury Plain, a wide expanse of beach east of Grace Glacier which was not divided into territories.

Late in the breeding season (February and March) territorial boundaries began to lose significance. Unsuccessful breeders left the area altogether before those which were completing the rearing of their chicks; when one member of a pair departed the other no longer defended its property with conviction, and newly fledged chicks and wandering birds as well as neighbours, could move into the territory without interference. Pairs with chicks frequently transgressed their neighbours' boundaries before either neighbour had left, the adults battling where necessary while the chick wandered or ate. The most persistent and damaging fights of the year were seen at this period, although they still lacked the violence which might be expected of so rapacious a bird. All territorial behaviour was abandoned by mid-March, shortly after the last of the locally bred chicks departed; details of the parents' departures during March and early April are given in Section 2i.

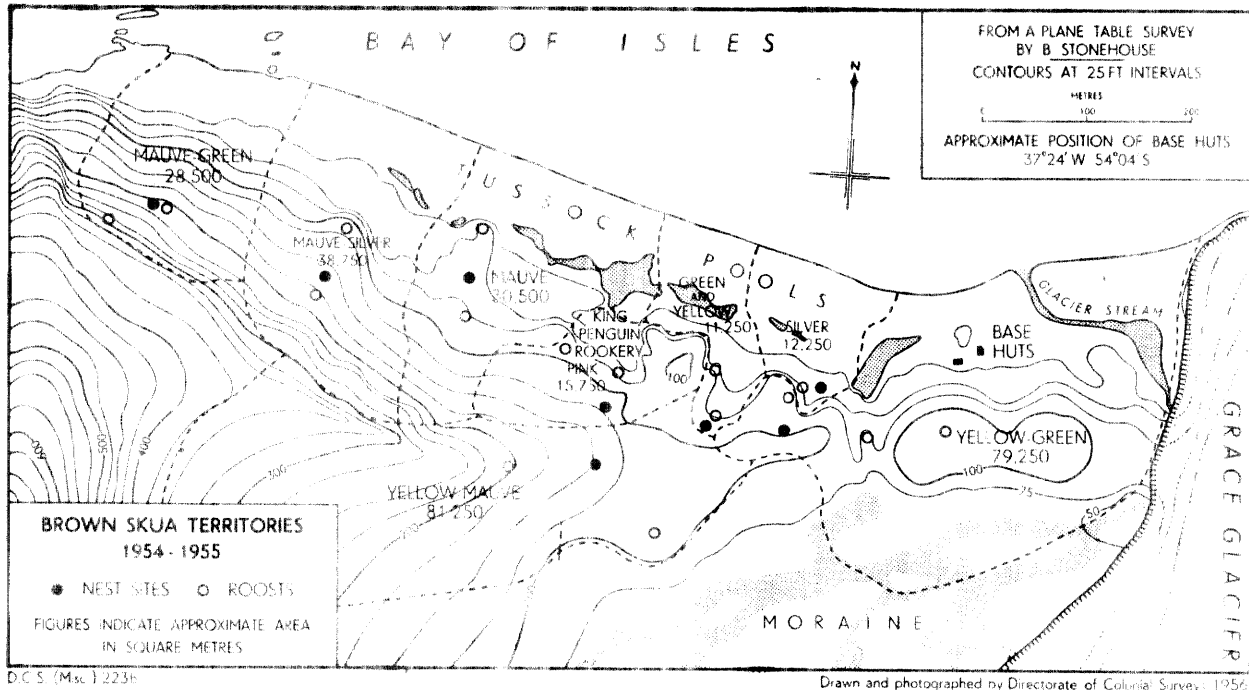


FIGURE 3. Brown Skua territories, 1954 - 1955.

In the second season the territory pattern was basically similar to that of the first year (Fig. 3). As each colour-ringed bird returned to the beach from migration it was found almost exclusively in its territory of the previous year, although occasional use was made of adjacent ground until its owner returned. Again very few boundary disputes were seen, the old boundaries being recognised as soon as both territories were reoccupied. Two new territories were, however, carved out of existing ones. That of the Mauve-Silver pair was occupied by a lone bird at a time when Mauve Right was also unpaired; later the lone bird paired and the two were banded. They occupied the western half of the previous year's Mauve territory. Although this area had been defended by the Mauve pair and was frequently entered by their chick in its excursions from the vicinity of the nest, most of their activities had been confined to the eastern half where the penguin rookeries were to be found. In addition, a small strip of the previous year's Green-Mauve territory was annexed, an unimportant stretch where the boundary was somewhat indeterminate. Silver territory arose from the absence of two of the previous season's breeding birds, Green Right and Yellow Right. The two remaining birds paired after initial antagonism, making use of the old Yellow territory and a little of the old Green territory borderland. The space remaining was later filled by a stranger who acquired a mate, the two becoming the Silver Pair.

The ease with which the two new territories were apparently formed suggested that the area could, if necessary, have supported more breeding birds. There was, for instance, no obvious reason why the eastern half of Yellow-Green territory should not have accommodated another pair. It is perhaps significant that both the Yellow-Greens returned early in the second season to breed, forming a particularly alert and belligerent team. Gulls attempting to settle there in the second season mobbed the Yellow-Greens when they flew in the area, but did not succeed in building nests and finally left altogether. An unmarked bird seen frequently to settle on the ridge which marked the northern boundary of Yellow-Mauve territory, was just as frequently driven off by the owners which were occasionally assisted by Mauve Right. In fact, territories in which both the previous owners returned early remained intact; those in which only one returned suffered alteration. This suggests that the time interval between the return of a partnerless bird and its acquisition of a new mate is a critical period during which the unaccompanied owner is unable to defend its territory satisfactorily against the settling of single interlopers. Once settled the interloper too acquires a mate and the two pairs exist side by side without further trouble, taking as a territorial boundary some natural feature or its projection toward the sea.

The territory of a Brown Skua is therefore primarily a place in which to live and rear chicks without interference. Secondly, it is a place in which to feed; a territory containing a Gentoo Penguin rookery provides an assured food supply once the Gentoos have started to lay, but there is no evidence that skuas which do not own penguin rookeries as part of their territory are at a disadvantage in feeding their chicks. A territory once held seems to remain the property of the holder throughout its life; whether or not it includes a rookery in any particular year is probably a matter of chance; Gentoos tend to shift their nesting sites from year to year.

e. Pairing

In the first season, all the pairs were established before observations began. All the breeding birds were then marked, so that in the second season I could follow their behaviour from the moment of return. The first two or three birds to be seen were unmarked strangers, arriving in the first week of September. On the 15th of that month fourteen unmarked birds were seen on the cliffs, occupying roosts in Yellow and Green territories but showing no territorial behaviour. On the 17th, Mauve Right returned and took up its old position above the headland. An unmarked bird was seen in its company, settling at a distance of twenty metres, flying off when Mauve Right flew off, but taking no part in defending the territory against casual interlopers. Two days later, this bird was seen to give challenge displays antagonistically at passers-by. For the next few days the two shared the territory, steadily driving off intruders on the rookery side of the headland but ignoring the lone bird which had moved into the western half of the old territory. Their behaviour was as yet unco-operative, and Mauve Right was frequently seen engaged in a low intensity threat display (challenge-walking) with the unmarked bird behaving submissively in response. On 25th September, Mauve Right was seen displaying at birds flying overhead and pulling at tussock grass the tips of which were just beginning to appear through the snow; by the end of the month the two were roosting closely together and behaving as a well-established pair. This was the first new pair to form; in the previous year the Mauve pair was slightly ahead of the others in breeding.

Mauve-Green Left was the second marked bird to return; it appeared on 18th September on its old roost. It was seen to chase off intruders during the following week, and to acquire a succession of temporary partners which again remained at a distance although clearly in association. A permanent liaison with a new partner was established by 20th October. Its partner of the previous year did not return.

Green Left appeared on the 20th September, disputing the possession of the eastern end of the King Penguin rookery with its rightful owner, Pink Right. Pink Left was also present, but the two Pink birds, which had arrived on the same day, were completely unco-ordinated in defence of their territory and both submissive to Green Left. By 25th September, however, the two Pinks held their end of the rookery against all comers and behaved as a pair, and Green Left had retired to its old territory.

The Yellow-Green pair appeared together in their territory on 23rd September; again they seemed wary of each other and defended their territory independently for the first few days. On the 25th both left their territory, flying high along the coast and later returning independently. By the 28th they were again behaving as a pair.

Yellow Left was seen for the first time on 26th September, sitting on its own side of the old territory boundary with Green Left nearby. The two showed slight antagonism but none of the enmity of the previous year. For a week they remained apart, each patrolling its own territory, with Green Left frequently appearing in and being driven from other territories. By 8th October the two were starting to fly together; by the 19th they had formed a pair, roosting in the old Yellow territory and seldom straying from it.

Yellow-Mauve Left appeared on its old roost on 30th September. Seen in company with Green Left in the same place on 3rd October, it was joined by its old partner on the 5th, and the two followed the usual pattern of pairing after an initial spell of wariness.

The Mauve-Silver and Silver pairs were late in forming. Mauve-Silver Right is believed to have been the first arrival, although neither was marked until the pair had formed. This bird remained alone throughout the last week in September, demonstrating against passers-by and occasionally permitting another bird to share the territory at a distance; on 7th and 8th October a settled partner was seen sharing the roost and displaying against interlopers on the beach. The pair was firmly established by 13th October and subsequently laid a single egg.

Also on 13th October a stranger was first seen in the old Green territory, calling from a ridge east of the old nest site. It remained alone until 14th November, when a temporary liaison with another stranger was

established. Throughout this period it defended its area alone, seldom coming into conflict with any of its settled neighbours. On 7th November it was introduced to its reflection in the mirror with food in front of it. The bird approached the food, jumped when it saw its reflection, and stood poised ready for flight with collar feathers erect. It started a challenge display but broke off, then walked to and fro past the mirror in a challenge-walk as previously described. It then approached its image with head lowered, and wings slightly extended, and beak raised in the manner of a begging chick. It dug its beak into the ground a few times in a submissive manner, then flew back to its roost. This bird was later assumed to be the male of the pair, its partner, which was acquired on the 23rd, being larger and "retiring" just before the egg was laid. Courtship and nest-building started immediately on the arrival of the new bird and the single egg was laid five days later, by which time most of the other birds were incubating. This became the Silver pair.

f. Courtship, Nest-building and Laying

The Yellow-Green pair, in whose territory the expedition base had been built, was most frequently under observation during the courtship period. After pairing on return to the territory they were seldom seen out of each other's company, combining to keep the territory clear of intruders, advertising their joint presence to strangers flying overhead, and feeding together on household scraps and seal debris. Sexual behaviour was not seen until 28th October, when the pair had been well established for about five weeks. At 1830 hours (local time) both were feeding on the beach. One started a short continuously repeated call, fluttered onto the partner's back, and stood there precariously for a few moments, still calling. The other apparently ignored these activities and continued to feed undisturbed. The call was heard again from time to time in the next few days and at 2000 hours on the 28th another attempt was seen; Yellow-Green Left called and made several attempts to flutter on to the partner's back. Yellow-Green Right moved away each time, then stood by begging with neck lowered and beak slightly raised in an attitude previously seen only in fledglings. The beak was moved slightly in a vertical plane and a soft piping call was heard above the interrupted call of the mate. Yellow-Green Left regurgitated food, which was gobbled rapidly; more food followed and again Yellow-Green Right ate it, this time digging its beak firmly into the snow. Yellow-Green Left fluttered up on to its partner's back once again. The partner settled on the snow, then shifted rapidly as the upper bird's tail was brought around to the left and downwards. Yellow-Green Left fluttered off, landing in the snow two metres away and treading repeatedly with both feet, its tail brushing the snow behind in rapid lateral movements. The two stood for some minutes making small "head-flagging" movements (Tinbergen 1953a, p. 31), then both flew off. They were again seen copulating in the afternoon of 4th November, Yellow-Green Right occasionally pecking upwards at the fluttering partner. On the 8th, at 1030 hours, Yellow-Green Left was seen to feed its partner on the beach after the partner had begged, and on the 9th at 20:00 hours they were again seen to copulate. On the 12th at 1700 hours, copulation was again preceded by begging and regurgitation. Throughout this period Yellow-Green Right was not seen to feed directly at all; Yellow-Green Left invariably regurgitated if caught feeding by its partner. Up to the 20th no nest had been discovered, but it seems likely by comparison with other pairs that one or two preliminary nests might have been made between the 12th and the 20th.

An attempted copulation was also seen in the Pink pair; Pink Left gave the call for four minutes, and Pink Right was seen to salivate but otherwise make no response. Pink Left attempted to mount, but its partner turned away and flew off.

On 20th November, a nest with one egg was found in Yellow-Green territory twenty metres from the site of the previous year. Two partially completed nests were close by. A second egg was laid on the 22nd-23rd of November. Thus about eight weeks elapsed between the return of the pair and the laying of the first egg; sexual behaviour was seen only in the last three and a half weeks of this period.

The presence of nests was indicated when a pair started to defend a particular area by swooping low as the observer approached. By 8th November, all except the Yellow-Greens and the unpaired Silver bird had two or three nests partially formed within two metres of the final nest site. In no case was the previous year's site reoccupied. Typical sites were on elevated grassland, with the nest itself usually raised slightly above the general level and shielded by long grass. Nests were flattened by repeated stamping and settling on one small patch of turf, and lined with grass plucked from the adjacent area. Both birds took part in nest-building, usually with one bird, which was probably female, sitting on the nest for most of the time. Building was intense and spasmodic, an adequate nest being made in about twenty minutes of concentrated activity.

For two or three days before the first egg was laid Yellow-Green Right was seldom seen about the territory. She could always be found near the nesting sites and was prepared to challenge passers-by, but did not fly actively in defence of the territory. This period of "retirement" was also noted in other pairs, and was a good indication of when the first egg was likely to arrive. The retiring bird, always the more bulky of the pair at this stage, remained comparatively inactive until the second egg was laid; in cases where both defended the territory with equal fervour no second egg appeared. As more clutches of two were found in skua nests away from the area than were seen in the eight nests under constant survey, it is possible that visits by the observer inhibited the laying of a second egg in some cases. Only the Mauve pair failed to lay at all in the second season, although they made three nests on their headland between 29th October and 7th November. After mid-November they abandoned the nesting ground altogether and spent all their time sitting above the Gentoo Penguin group higher up the hill.

Stolen eggs were not replaced. Removal of a first egg did not interfere with the laying of a second, and removal of either first or second eggs did not prompt the laying of a third. The addition of an egg to a nest already containing one did not inhibit the laying of a second egg.

Table III summarises egg weights, measurements and nesting successes in both seasons. Eggs were only just hatching when the base was relieved in December, 1954, but the beach was revisited in mid-January and all the territories were searched for chicks.

g. Incubation and Care of the Young

Two or three days elapsed between the laying of first and second eggs. During this period the suspected female was usually to be found incubating, leaving the nest for short periods only. An uncovered nest was invariably occupied immediately by one or other of the birds unless both were actively defending the site. After the appearance of the second egg the partners alternated at intervals of a few hours, possibly with some degree of regularity. For example, during the first season Yellow-Green Right usually appeared before the hut window in time to catch the breakfast scraps at 0900 hours, and its partner usually fed on a seal carcase down on the beach between 0800 and 0830 hours. The guard was changed with little ceremony, the incubating bird rising on the approach of the partner and stepping quietly off the nest if ready for relief. Newly relieved birds were frequently seen to walk immediately down to a pond to drink and paddle; later, they would feed, challenge from their roosts or patrol their territories. If disturbed on the nest both birds would fly up to attack; frequently the bird which had been incubating would find the nest occupied by its partner after the alarm had passed.

During the first few days of incubation both birds seemed eager to incubate whatever the weather. An exception was the case of the Mauve-Silver pair, whose egg was seldom covered and was quite cold for the first four days, which happened to be mild. As incubation progressed, nests were frequently left by both birds on warm, sunny days. None of the eggs was stolen during these periods of absence. On wet or cold, windy days the birds incubated closely. Temperatures of eggs and egg cavities, measured with a "Thermistor" probe during incubation, are shown in Table IV. The eggs were olive-brown, splashed with brown-purple and grey flecks, but Gentoo eggs, larger than their own and white, were accepted for incubation by any of the skuas if placed within ten centimetres of the nest (Plate IIb). Within half a metre of the nest, King or Gentoo eggs remained untouched, the birds showing considerable interest and occasionally salivating copiously but making no attempt to crack them. Away from the nest, eggs of any species were likely to be eaten.

As it seemed probable that only one chick was normally reared from a clutch of two eggs (Murphy, *op. cit.*, p. 1027), second eggs were in most cases removed early in incubation for embryological and growth studies. The cause of death of the second chick was therefore established in only one case; unfortunately the second season was later than the first and observations ceased before any of the double clutches of that year were hatched. In the one recorded case (the Yellow pair) the eggs hatched within forty-eight hours of each other. The first chick was apparently not fed in the intervening time and was found squashed alongside the nest on its second day. Murphy's view that only one chick elicits parental care, the second being regarded as food once the first has been tended, is discussed later (see Section 3b). There was no evidence to suggest that neighbouring pairs showed particular interest in each others' nests or chicks; the Green chick was for experiment placed in Yellow territory on four occasions at weekly intervals from the age of twenty-one days. The Yellows gave full threat displays in front of it each time but did not attempt to touch it: each time the chick adopted a begging or submissive posture and was allowed to walk

unmolested from the territory. On the fourth occasion the chick, by this time fully fledged, gave a shrill alarm call as the two Yellow birds approached; its own parents, who had been given a seal steak on the beach to keep them away during the experiments, immediately flew up, found the chick at once and delivered a series of violent attacks on the Yellow pair, diverting their attention while the chick ran for cover. The Mauve chick was similarly respected by the neighbouring Pink pair whenever it ran into their territory, although its parents seldom allowed it to remain unattended in a foreign territory for long.

Three incubation periods, each of thirty-two days, have been recorded. In all observed cases the first cracks appeared two to three days before the chick was free of the egg, e.g. at the 29th or 30th day of incubation.

The chicks ran from the nest within a few hours of hatching, returning only to hide under an incubating parent. Within twenty-four hours of the second chick's hatching, the nest lost all significance to chick and parent. Chicks seldom moved far from the site, however, establishing runs for themselves with convenient corners under rocks or vegetation in which to crouch when alarmed. For the first few days the area roamed would be limited; later the chicks usually moved to another part of the territory altogether. Parents seemed always to know the exact location of their chicks; chicks were found for weighing and measuring by searching carefully where the parents' diving attacks were most persistent. On hearing the parents' alarm calls the chicks ran for a few yards to crouch motionless; their buff-coloured down blended well with the surrounding colours of faded vegetation and stones, and frequently the most diligent search failed to reveal them.

The Green chick was observed daily, and the earlier-hatched Mauve chick at intervals of two to three days. Both spent most of their time lying in the short tussock grass, occasionally running to another covert or pecking apparently aimlessly in the turf. A returning parent was greeted with a persistent low-pitched whistle, accompanied with slight upward movements of the beak, to which the parent responded almost immediately by regurgitating food onto the ground at the feet of the chick. Begging continued until a second or possibly a third supply was delivered, the chick chasing the adult with body horizontal, head low and beak elevated slightly. Food included krill, seal meat, penguin chicks and eggs. Frequency of feeding was not determined accurately, but both adults spent much of their time sitting quietly in the territory and watching the chick, and there was apparently no urgency or difficulty in feeding at this stage. Wandering chicks occasionally approached their sleeping parents, whistling and adopting the begging attitude. They were seldom successful in obtaining food immediately, but plagued the parents until they flew off to return later with a supply. As the chicks grew older and their feathering developed, food supplies were demanded more frequently; chicks were often heard whistling in the absence of their parents, who foraged almost continuously throughout the day. Newly fledged chicks hounded their parents on sight and wandered further afield; they walked in a characteristic attitude with neck and body almost horizontal, wings drooping slightly from their coverts and a generally furtive air which contrasted sharply with the upright and deliberate movements of parent birds. Parents were driven away from any food found in the territory; they seemed unwilling to eat if accompanied by the chicks and were actively prevented by the chicks' belligerent attitude in the presence of food. On 16th February, when the Green chick was fully fledged, a dead King Penguin chick on a long string was thrown over the cliff to where the Green parents were standing not far from the nest. The observer, on the cliff top, was out of sight and could move the chick slightly by pulling the string. The adults started feeding immediately; the Green chick, who had been sleeping under a clump of tussock, moved up in characteristic attitude, whistling persistently. Both adults immediately stood back while the chick pecked at random, grasping first a flipper, then a foot, and quite unable to make any headway. Green Left moved forward but was pecked by a rapid upsweep of the chick's beak. The string was pulled and the King chick moved a metre up the hill. Both adults dived forward and started to tear it, again stopping and standing back when the chick moved forward whistling plaintively. After half an hour the chick, still unable to break through the penguin chick's tough skin, lay alongside it keeping the parents away.

On the following day the three were together in the territory. I placed an egg in front of them and retired to watch. The chick advanced on the egg and foraged under it. Green Right approached and was driven away. The chick rolled the egg (a King Penguin's) but did not attempt to crack it. Both parents advanced, but again the chick drove them off, pecking at their breast feathers and legs. Green Left moved away, pursued by the chick in begging attitude, regurgitated a little food, and took advantage of the chick's momentary preoccupation to fly back and pierce the egg with a rapid and efficient jab of the beak.

Both parents ate, characteristically in turn, and the chick came up just in time to finish it off. The chick then pursued Green Right, who regurgitated its share of the egg, and all three ate rapidly. The chick hounded both in turn until they retired up the slope to their roost.

The Mauve chick flew on the fifty-eighth day after hatching; when approached by the observer it took off across wind, flew up and down the beach in the limits of its parents' territory calling continuously, and finally landed inexpertly on the hillside. Its parents appeared to recognise it in the air, possibly by its calls, and did not display at it. The Green chick was seen to flutter from the bank to the tussock, apparently unable to gain height, on the fifty-ninth day after hatching. When approached on the following day it took to the air after a short run, flew awkwardly with feet down calling continuously and attempted unsuccessfully to land in the tussock tops. It finally made an ungainly landing on the hillside after three inelegant attempts in other places. Flying techniques improved rapidly although the chicks seldom took to the air except when approached by the observer; they still tended to run and crouch when alarmed. The wings at this stage were frequently held half extended when walking, in the manner of a Giant Petrel. The adults came to spend more time away from their chicks, roosting high in their territories but still flying aggressively to their defence when necessary. By mid-March the chicks were flying more frequently and spontaneously and were often seen away from their territories. By the end of March all had left the area in the company of wandering groups composed largely of their contemporaries.

h. Growth of the Chicks

In the first season Mauve and Green chicks were weighed, measured and examined periodically from hatching. The dimensions recorded were:

Length of upper mandible from tip to gape with beak closed.

Length of foot from tip of middle claw to proximal end of tarso-metatarsus.

Length of extended wing (excluding feathering) from tip to axilla.

GREEN CHICK						MAUVE CHICK					
Date	Age in Days	Weight (gms.)	Length in cms.			Date	Age in Days	Weight (gms.)	Length in cms.		
			Beak	Foot	Wing				Beak	Foot	Wing
20.12.53	4	100	2.4	6.8	6.3	3.12.53	2	125	2.8	7.0	5.8
24.12.53	8	180	3.0	8.4	8.2	14.12.53	13	510	4.7	12.0	16.0
29.12.53	13	315	4.1	9.5	11.5	20.12.53	19	750	5.8	14.2	22.0
6. 1.54	21	660	5.3	13.4	24.1	24.12.53	23	1200	5.9	16.3	—
7. 1.54	22	750	—	—	—	29.12.53	28	1150	6.2	16.3	—
9. 1.54	24	840	—	—	—	1. 1.54	31	1500	—	—	—
12. 1.54	27	1050	—	—	—	9. 1.54	39	1700	6.2	16.5	—
15. 1.54	30	1200	—	—	—	15. 1.54	45	1700	7.0	16.5	—
17. 1.54	32	1300	—	—	—	18. 1.54	48	1700	7.5	16.5	—
21. 1.54	36	1500	6.3	16.5	—						
29. 1.54	44	1600	7.0	16.5	—						
1. 2.54	47	1600	7.1	16.5	—						
9. 2.54	55	1700	7.4	16.5	—						

YELLOW-MAUVE CHICK		MAUVE-GREEN CHICK	
Date	Weight (gms.)	Date	Weight (gms.)
10. 1.54	880	7. 1.54	540
22. 1.54	1300	23. 1.54	1500
2. 2.54	1400	29. 1.54	1400
		16. 2.54	1750

TABLE V. Growth and development of four chicks.

The last measurement was discontinued when the wings were almost grown, as extension involved a danger of **damaging** the structure. Two more chicks, belonging to the Mauve-Green and Yellow-Mauve pairs, were found for the first time some days after hatching. These were weighed and measured three or four times in the hope that their growth curves would fit the two more complete sets of data and give a reasonable estimate of the chicks' ages. Weights and measurements are listed in Table V, and the weights of the Green and Mauve chicks are shown as graphs in Figure 4. Their curves agree closely, although those of the Mauve chick (from a heavier egg) are clearly heavier throughout. So close a correspondence is probably fortuitous, and more weighing may have indicated fluctuations which do not appear in the present curves.

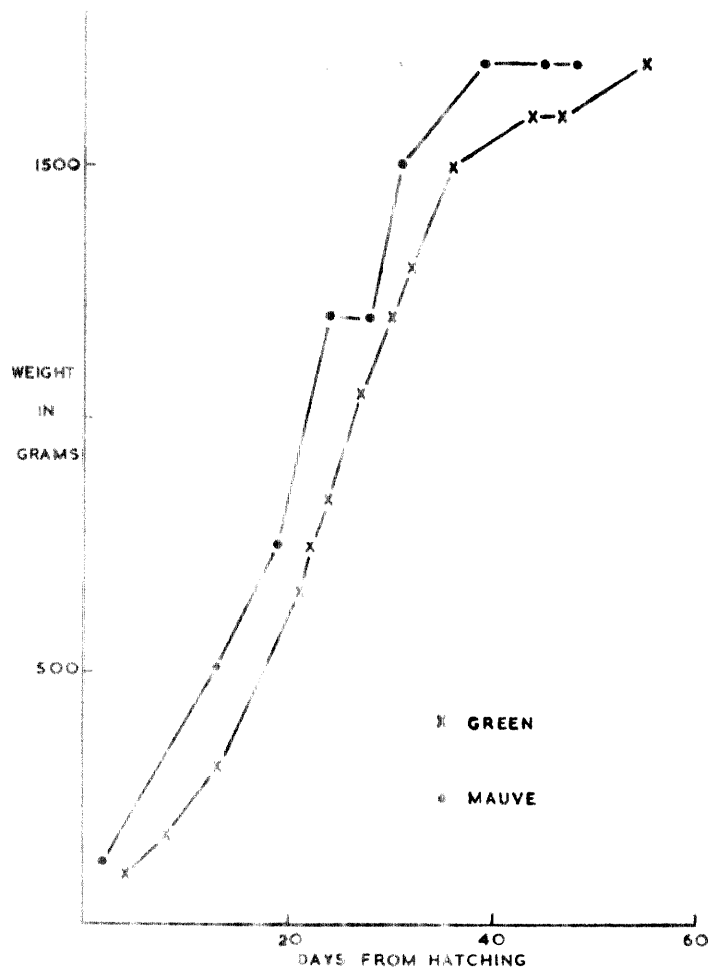


FIGURE 4. Weights of Green and Mauve chicks, from Table IV.

The following notes on plumage, growth and activities refer in particular to the Green and Mauve chicks, development of which was similar at all stages.

Both were hatched from single egg clutches, one egg having been removed from the Mauve nest at an earlier stage for embryological studies. Both chicks were seen on their first day with membranes still attached, but were not disturbed. The Green chick was still curled, the Mauve chick, a few hours older, was crouched in the nest probably heeding the parents' alarm calls. On the second day, the Mauve chick was hiding below a tussock patch one metre from the nest and was able to run when disturbed. Both were covered with fawn down, dense and paler at the roots; legs and beak were bluish grey, with white caruncle. Eyes were black with blue opalescent pupils. Both chicks were sturdy and active, crouching after a short run

in response to alarm calls, pecking when handled, and producing their own alarm calls which stimulated the parents to renew their violent attacks on the observer. The Mauve parents attacked invariably in swooping dives; the Greens, tamer and more accustomed to the presence of an observer, contented themselves with pecking and tugging at my windproofs or flying off with gloves and weighing apparatus. In the absence of their parents the chicks crouched when danger threatened; they wandered freely within a few metres of the nest, but frequently cocked their heads to view the sky and settled when a Giant Petrel or other bird passed overhead.

At thirteen days, the Mauve chick's wing quills appeared. On the nineteenth day, contour feathers were appearing. In both respects the Green chick was two days later. Down remained attached to the feather tips for as long as four weeks; by the fortieth day both chicks were covered although the feathers, particularly the quills, were still growing. By the fiftieth day they were running freely in the territories, generally avoiding the long tussock grass which covered the upper half of the beach. They ran with wings extended. As yet there was no strength in the pectoral muscles and, when folded, the wings dropped below their coverts giving the chicks their distinctively crouched appearance. Although fed mainly by their parents they were by this time feeding also from seal carcasses on the beach. The quills were fully grown about the fifty-fifth day, and flying started in both cases before the sixtieth day. However, it is possible that undisturbed chicks would not have ventured into the air until later, as very little flying was seen at first, and the chicks continued to run from danger, rather than fly, for another week.

i. Departure

Territories tended to lose their significance after mid-February, pairs with chicks expanding their feeding grounds by repeatedly trespassing on their neighbours' property. The Green family took control of the seal remains at the seaward end of the pool which had previously formed a boundary to their territory, then fed repeatedly in front of the hut where food was provided daily for the Yellow-Greens. The latter pair, both of whose eggs were apparently sterile, skirmished inefficiently for some time; on the morning of 23rd February, however, Yellow-Green Right fought and routed Green Right in a five-minute battle by the feeding tray, after which the Greens kept rigidly to their own grounds. Similarly the Mauve family scavenged further and further into the Pink territory on the King Penguin rookery.

At the same time the colour-ringed birds started to leave the Beach. Yellow-Right was not seen after mid-February, and its partner, which had dominated the Green pair throughout the season, suddenly became insignificant. On 18th February, Green Left accompanied me along the beach through its own territory, then through Yellow territory with Yellow Left fluttering behind making aggressive displays which were completely ignored. In the 18th, the two were seen in a boundary dispute by the nest sites: Green Left was gradually forcing Yellow Left back across the boundary in a series of threat displays. Yellow Left protested vigorously at first, then gave a submissive response to each of its opponent's calls, finally flying off to another part of its territory. The Yellow territory was also invaded from the other side although with less determination: the Pink pair, whose eggs were lost, occasionally chased Yellow Left from the roost and wandered at will on the Yellow territory beach. They disappeared simultaneously on 4th March, and immediately Yellow Left and the Green pair moved into their corner of the King Penguin rookery to feed on abandoned eggs and dead chicks.

As the territories cleared, more of the wandering birds came in to feed; most of these were juveniles, probably fledglings, in dark unfaded plumage and with incomplete or inadequate display behaviour. They were chased uncompromisingly from occupied territories, but found themselves on equal terms with colour-ringed trespassers in those from which one or both owners had disappeared. By 11th March, Mauve Left and the chick had gone and Yellow Green Right was also missing; both these territories were invaded, and defended only spasmodically by the remaining owners. The invaders sat in close knots about the feeding grounds, occasionally shifting slightly when challenged by an owner but settling again as soon as trouble had passed. On 15th March the Green chick was no longer about, Green Right still occupied the territory, and Green Left had moved almost permanently into Pink territory, using the old roost and feeding on the rookery floor in company with Yellow Left. These two were apparently on good terms, tearing food together and sharing newly found eggs as though a long-established pair. On 17th-18th March a strong southwesterly gale blew, and most of the remaining skuas disappeared overnight. Green-Mauve Right was the last to go, on 25th March. Wandering birds were seen about the beaches and rookeries throughout April, feeding in groups in which peck-orders were apparent but no territorial behaviour was seen. The

population thinned during May; food was still abundant and the remaining birds were plump and weighed about two kilos. By the end of May only one bird remained, and this disappeared in the first week of June.

With the breeding birds, departure followed a short period of partial moult; the quill feathers were replaced with very little alteration in the birds' appearance. Green Right and Green-Mauve Right were late in starting their moult, and were the last to migrate. It was extremely difficult to diagnose the moulting condition, but no displaced or lost quills were seen after the breeders had gone and it seems likely that the juveniles did not moult at all before leaving.

Section 3

DISCUSSION

a. Comparisons with other stocks of Brown Skuas

REFERENCES to Brown Skuas appear frequently in the literature, but in few cases have prolonged studies been made. It is difficult to assess the value of Wilson's observation (1907, p. 64) that the Brown Skuas of Macquarie Island gave a distraction display, or of Buller's statement that a captive bird from the New Zealand area was seen to hold down prey with its feet while tearing with its beak. Both patterns of behaviour were carefully watched for on South Georgia but neither was seen. Further evidence on the presence or absence of clearly defined behaviour patterns of this nature, would help considerably in determining the relationships of these birds. A most interesting series of comparisons has been supplied by Dr. L. E. Richdale from his unpublished observations on the skuas of Stewart Island and neighbouring islands off the coast of New Zealand. He reports seeing on more than one occasion three adults (of unknown sex) in one territory, and mentions that in most cases two chicks are reared by each breeding pair. The nests are generally as far apart as those of South Georgia and the general behaviour of the birds is similar.

Feeding habits seem to vary according to the opportunities presented. Skuas are invariably present on any penguin rookeries within their range, and are often to be found in association with small nocturnal petrels of various species. The diurnal and ubiquitous Pintado Petrels were never molested by Brown Skuas in South Georgia. Terns, which frequently mobbed those skuas in whose territories they were nesting, were similarly immune from skua attacks, although South Georgia Teal (*Nettion georgicum* Gmel.) were frequently chased when they flew through the territories. Predation on rats has already been mentioned; Hall (1900, p. 9) reported that on Kerguelen the skuas habitually took rabbits, effectively controlling the population.

b. Comparisons with Related Species

Brown Skuas are members of the well-defined family Stercorariidae, which includes, in two genera, jaegers (*Stercorarius*) and skuas (*Catharacta*). Closely allied to the gulls, and resembling them in form and in many of their behaviour patterns, the jaegers and skuas agree in their more or less brown colouring, their predatory and generally dominating characters, and their ability to live parasitically on the efforts of other birds by chasing them in flight and forcing them to disgorge food in mid-air. They breed socially (not, as is generally stated, colonially) in polar and temperate regions mainly where rich seas provide food for large colonies of other sea-birds. They may also be dependent on small mammals. Detailed studies of their life histories are in most cases lacking, but recent work on Pomarine and Arctic Jaegers, in addition to widely scattered references throughout the literature, provides bases for comparison of the various members of the family.

Great Skua. Territories are usually closely packed. Perry (1949) quotes fifty-eight yards as an average distance between nest sites. Isolated pairs are also frequently recorded. The birds feed away from their territories, mainly on Kittiwake eggs and chicks (Lockie 1952, p. 160) in Scottish localities, and on a variety of local birds including fulmars (*Fulmarus g. glacialis* (Linn.)) in Iceland (Gudmundsson, 1954). Icelandic birds also feed on surface fish and offal, and the size of population may have fluctuated with increasing and, later, decreasing trawling activities since the beginning of the century. Two eggs are laid and both chicks

are usually reared. Mr. C. Mylne, in a personal communication, mentioned that he had not seen a distraction display in this species, and that second clutches are laid after nest-robbing in Shetland.

Chilean Skua. Little is known of this subspecies, which apparently lays two eggs (Housse 1942, p. 381) and nests in isolation.

McCormick Skua. Wilson (1907, p. 70) records seeing these birds in colonies, usually associated with Adélie Penguins (*Pygoscelis adeliae* Homb.). During three years in southern Graham Land, I have observed many isolated breeding pairs; some lived at the expense of Adélie Penguins, but others did not appear to be associated with concentrations of other species and were probably living exclusively on seal carcasses near the F.I.D.S. base. Two eggs are laid; Wilson mentions fights between the chicks and the early disappearance of one from each clutch. I was never able to record the survival of more than one chick from any clutch.

Pomarine or Pomatorhine Jaeger (*Stercorarius pomarinus* (Temm.)). Pitelka *et al.* (1955a and b), studying a population at Point Barrow, Alaska, found that the numbers of birds, and hence territory size, varied with cyclical fluctuations in numbers of Brown Lemmings (*Lemmus sibiricus*) on which they preyed almost exclusively. Nesting was not seen at all during 1951 and 1954, which were years of few lemmings; in 1952 territories were typically of about 110 acres with 2500 feet (a modal figure) between nest sites. Lemmings were plentiful in that year; 1953 was a peak year for lemmings, and the territory size of the jaegers was reduced to eighteen acres with about 1000 feet between nests. Approximately four to five times as many pairs bred in 1953 as in 1952. The birds hunted almost exclusively within their own territories; nesting success was probably lowered by the more crowded conditions. Families extended their territories in mid-summer, probably as a result of the lemming shortage at that period. No distraction display was seen; generally behaviour was similar to that of the Brown Skua.

Arctic Jaeger (*Stercorarius parviticus* (Linn.)). Williamson (1949b *et seq.*) has studied populations of this species for a number of seasons on Fair Isle. Marked birds have been found to return yearly to the same sites and partners. Territories are closely grouped (Perry (1948) gives an average distance of seventy-seven yards between nests in Shetland); staple foods are fish pirated from kittiwakes and other sea-birds. Two eggs are normally laid; Williamson records 42%, 69% and 90% rearing of both chicks in three successive years. Families tend to move their territories away from nearby Great Skua nests as the chicks develop; there is a marked distraction display (Williamson 1949a), the value of which Lack (1932, p. 67) questions in relation to possible predators on Bear Island and, indeed, within most of the birds' breeding range. Gudmundsson (1954) reports that territories in Iceland may be grouped or widely spaced according to the terrain.

Longtailed Jaeger (*Stercorarius longicaudus* Vieillot). Little information is available on this species, which seems to resemble the Pomarine Jaeger in most respects. Some authorities mention a distraction display; the birds are apparently territorial, feed mainly on small mammals while breeding, and lay two eggs. S. J. Davies and C. H. Fraser Rowell observing near Selkavaara (Swedish Lapland) in 1955, reported finding four nests each with one egg. Territories adjoined, each covering an area of one to two square miles. Food pellets contained remains of voles, reindeer hair, Ericaceous seeds and *Empetrum* berries (personal communication).

Territorial behaviour is common to all members of the family, but the actual significance of the territory varies considerably from species to species. Pomarine and Longtailed Jaegers feed within their territories during the breeding season; the average size of territory in the Pomarine Jaeger has been shown to vary considerably with the density of the species in any year, the density in turn varying with cyclical fluctuations in the abundance of lemmings. Arctic Jaegers, when feeding on microtines, may similarly be controlled. It seems, however, that this species depends more on marine sources for its feeding and in most cases the territories are used solely for nesting. Arctic Jaeger territories are significantly smaller, in these circumstances, than are those of the other two Jaeger species; they are also more closely packed and localised within easy reach of food supply.

The Great Skua in Shetland and elsewhere follows the pattern of the Arctic Jaeger, feeding away from the territories which are again small and closely packed. The McCormick Skuas observed by Wilson were apparently similar, but those observed by me were undoubtedly feeding and nesting in large territories remote from each other. Brown Skuas and possibly Chilean Skuas are also in the latter category; the

Brown Skuas seen in South Georgia seemed to be basing their economics on the probable presence of Gentoo Penguins in their established territories, being sufficiently versatile to be able to breed successfully in those years when the penguins are not present. In the possession of this quality they differ fundamentally from Pomarine Jaegers, which do not breed during years of lemming scarcity.

The tendency for skuas and jaegers to lay two eggs and rear only one chick is also worthy of comment. Williamson (1949, p. 25) reports a case in which one of a brood of Great Skua chicks did not respond to its parents' invitation to feed, and died of starvation. Perry (1948, p. 85 *et seq.*) gives evidence of bad weather and predation accounting for the deaths of half the chicks belonging to 113 pairs of Great Skuas; the pairs were assembled in groups from some of which no chicks were lost at all while from two other groups 44% and 37% were lost. Isolated pairs of Arctic Jaegers were less successful than were those breeding in groups, mainly because of the activities of predators (*op. cit.*, p. 171). Williamson (1951a, p. 238), discussing the same species, mentions that two chicks of a brood are antagonistic when placed side by side for plumage comparisons, and Wilson's record of fighting in McCormick Skua chicks suggests a similar tendency. Murphy's interpretation, previously quoted, would suggest a lack of plasticity in the behaviour of the Brown Skua which is not generally characteristic of the species, but further investigation is required before it can be judged whether the death of one chick from each brood is related to feeding difficulties in any locality or to innate behaviour patterns in adults or fellow members of a brood.

All skuas and jaegers are migratory, leaving their territories shortly after their chicks achieve independence and returning from four to eight weeks before the start of the next breeding season. The intervening time is apparently spent at sea (Wynne-Edwards (1935, p. 298) for Pomarine and Longtailed Jaegers, Witherby *et al.* (1941 *et seq.*) for other northern species). Migrations may also be extensive; Sladen (1952) records an Arctic Jaeger in the Antarctic, and Murphy (*op. cit.*, p. 1007) records the taking of more than one McCormick Skua in Japanese waters.

c. Comparisons with Gulls

Tinbergen's account (1953a) of the Herring Gull (*Larus argentatus argentatus* Pontopp.) provides many points for comparison; the behaviour of the Brown Skua is seen in general terms to be that of a gull from which social elements have been removed, and to which have been added other elements fitting the birds for their more solitary life. Typical releasers of social behaviour, the "call note" and "alarm call" (*op. cit.*, p. 10) are absent from the Brown Skua repertoire; the "trumpeting call" and "charge call" are represented in skua challenge calls and alarm calls when flying to attack. "Choking" in the gull may correspond with the conversational quack of the skua, an antiphonal call indicating uneasiness or low-intensity alarm; this call was occasionally heard between paired birds at a nest site but the actual circumstances and significance were not discovered. Food-begging behaviour in courtship and the male copulation calls are very similar in the two species. Most of the threat behaviour described by Tinbergen can be recognised in the skua; in the latter species, however, emphasis is laid on energetic defence of an established territory rather than on the establishment of balanced relations with other birds of the same species, and the threat postures are seen in paired Brown Skuas only during the short period between the return of migrants and their re-acceptance of territorial responsibilities. Once the territories have been taken up, the isolation of the birds reduces the necessity for threat postures other than the challenge call.

The presumably cryptic coloration of the Brown Skua is also typical of a non-social animal; it is perhaps significant that, in a family in which all species and subspecies are notable for colour variation, it is the more sociable jaegers which show marked colour dimorphism as well as seasonal colour variations (Southern 1943, 1944). A special advertisement decoration, the wing-bar common to skuas and used in the full display which accompanies the challenge call (Plate I), is less prominent as a feature of display in the jaegers.

It is interesting to note certain other qualities which seem to be associated with the more independent type of breeding. The Brown Skuas of South Georgia and the McCormick Skuas of southern Graham Land, were, as individuals, remarkably alert and self-sustaining creatures which seemed far better equipped to deal with varying circumstances than were the gulls with which they came into competition from time to time. They missed fewer opportunities for feeding, responded more quickly and certainly to the extra feeding afforded by the presence of man, and were less responsive to the alarm calls and movements of other members of their species than were the ever-timid and ever-alarmed gulls.

d. Relations with "Host" Species

Brown Skuas in South Georgia appear to feed their chicks almost exclusively on food which Gentoo Penguins supply to their young. For this to be possible every year, some co-ordination in the time of laying is required between the two species. In the two breeding seasons studied there was evidence for such a co-ordination. The second season was about two weeks later in both species; Gentoos start their nesting behaviour as their sites clear of snow, and the snow cover persisted for about two weeks longer in the second season than in the first. In the second season skua eggs were not laid until the first of the Gentoo eggs were laid, and it seems likely that a similar condition existed in the first season too. In both years the first chicks of both species emerged at about the same time, the Gentoo incubation period being about four days longer than that of the Brown Skua (Gwynn, 1953, p. 10). There was no evidence that the skuas were held up for the same reason as the Gentoos (i.e. persistent snow cover) in the second season; they were apparently ready to breed for two or three weeks before they actually started and it is difficult to say why they did not unless their own laying was in fact determined by the laying of their "hosts". The King Penguins started laying on 25th November in both years; this was, however, later than the laying dates of Gentoos and skuas in both years and it is possible that by that time the lateness of the beginning of spring in the first season was of no account. More evidence is needed, but it seems possible that a physiological link may be present relating such a "parasite" to a host on which it may depend so closely. A similar state of affairs is reported in the two years studied by Fitelka *et al.*, where both lemmings and Pomarine Jaegers related their breeding seasons equally closely.

SUMMARY

A POPULATION of Brown Skuas (*Catharacta skua lönnerbergi* (Mathews)) on South Georgia was studied in the 1953 and 1954 breeding seasons. Breeding birds were colour ringed in the first year; where both survived it was found that they returned to the same territories in the second season to re-form old partnerships. The birds were strongly territorial but little boundary fighting was seen; boundaries were basically the same in both years although the area held two extra territories in the second year. Taxonomics, the habitat, feeding, antagonistic displays and breeding behaviour are discussed, and behaviour is compared with that of other skuas, jaegers and gulls.

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a



b

- (a) The beach near the base hut in summer, from the eastern end.
(b) Challenge display. The Yellow pair on their cliff-top roost.



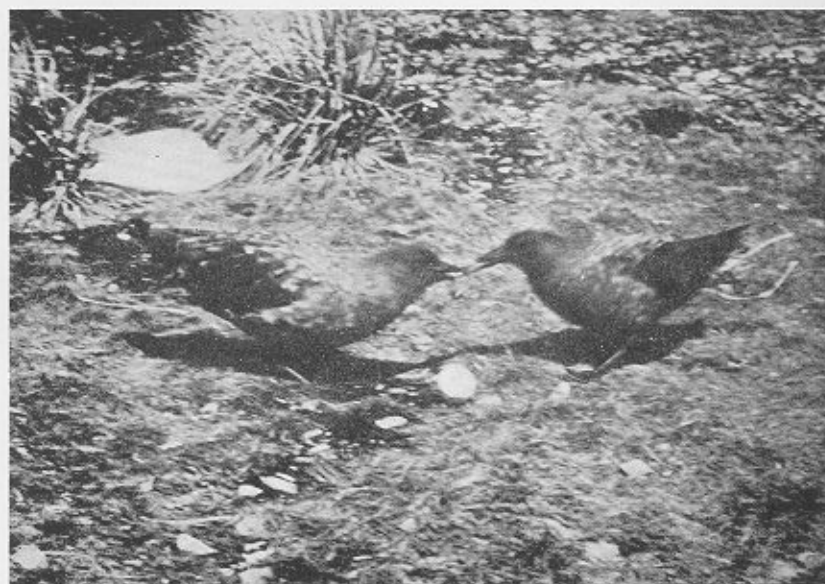
a



b



c



d

- (a) Yellow Left incubating.
(b) The Green pair with a Gentoo egg.
(c) Green Left settling on a Gentoo egg alongside its own.
(d) The Green pair tearing a Gentoo embryo.