

AGONISTIC BEHAVIOUR OF THE BROWN SKUA, *Catharacta skua lönnbergi* (Mathews)

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ABSTRACT. At Signy Island, South Orkney Islands, the territories of the brown skua (*Catharacta skua lönnbergi*) are large and the birds concentrate their activities around the roosting sites and nests. Non-breeding skuas gather in clubs where hostile and apparent pairing behaviour was observed.

The intraspecific agonistic behaviour of *C. skua lönnbergi* is very similar to that of other subspecies of *C. skua* that have been studied. Some displays are shown to be caused by different levels of motivation and by different stimuli, but they do not appear to convey different levels of threat. It is suggested that the skuas (Stercorariinae) have fewer displays than gulls (Larinae) because the lower nest density of the former reduces the pressure to ritualize hostility.

Predation of skua broods by other skuas is very slight at Signy Island, reactions to other skuas serving mainly to space the population. A human intruder evokes an increasingly stronger hostile reaction as he approaches the nest. Weather, state of the brood, incubating tendency and absence of the mate affect this reaction. Little is known of the predators of *C. skua*, apart from congeners and Man, but it is likely that most predation is on the brood. The anti-predator reactions are adapted to reduce this.

THIS study was carried out at Signy Island (lat. 60°43'S., long. 45°38'W.), South Orkney Islands, from December 1963 to March 1966 while I was serving as a meteorologist at the British Antarctic Survey station. In previous years nests had been mapped and many of the breeding skuas colour-banded. This work provided a basis for a study of the cause and effect of displays and of territorial defence.

Taxonomic note

The family of skuas (Stercorariinae) includes four species:

Stercorarius pomarinus: the pomarine skua.

Stercorarius parasiticus: the Arctic skua.

Stercorarius longicaudus: the long-tailed skua.

Catharacta skua: the great skua.

The great skua has been subdivided by Hamilton (1934) into five subspecies:

C.s. skua: the great skua of the North Atlantic.

C.s. chilensis: the Chilean skua of South America.

C.s. antarctica: the Falkland Islands skua.

C.s. lönnbergi: the brown skua of sub-Antarctic and Antarctic islands.

C.s. maccormicki: the South Polar skua of the Antarctic continent.

INTRASPECIFIC AGONISTIC BEHAVIOUR

General description

Displays of great skuas have been described by other authors. Moynihan (1962) studied the Chilean skua (*C.s. chilensis*) and Perdeck (1960) described the great skua of the North Atlantic (*C.s. skua*). In this paper names of displays are based on those used by Moynihan; those not previously described are given purely descriptive names. All names of displays are designated by italics. A comparison of the names used here and by Moynihan and Perdeck is given in Table I. Detailed descriptions of the forms of displays (shown in Fig. 1) will not be given here except to compare *C.s. lönnbergi* with other subspecies of *C. skua* and with gulls, and where there is no previous description.

However, no account of behaviour is complete without reference to the overall habits of the species. The breeding (about 100 pairs) and non-breeding populations of Signy Island have been described in a previous paper (Burton, 1968). The territories are large and the nests widely spaced, ranging from 60 to 700 m. apart. There are few boundary disputes as the skuas

TABLE I. GLOSSARY OF NAMES OF SKUA DISPLAYS USED BY DIFFERENT AUTHORS

<i>This paper</i>	<i>Moynihan (1962)</i>	<i>Perdeck (1960)</i>
<i>upright</i>	<i>aggressive upright</i> <i>anxiety upright</i>	<i>aggressive upright</i> <i>intimidated upright</i>
<i>gape</i>	<i>gape</i>	
<i>long call</i>	<i>long call</i>	<i>long call</i>
<i>high oblique</i>	<i>high oblique</i>	} <i>oblique with wing raising</i>
<i>normal oblique</i>	<i>normal oblique</i>	
<i>low oblique</i>	<i>low oblique</i>	
<i>very low oblique</i>	<i>very low oblique</i>	<i>bend with wing raising</i>
<i>bent neck</i>	<i>bent neck</i>	<i>bend</i>
<i>stifled long call notes</i>	<i>rusty squeaks</i>	
<i>bill down</i>	<i>bill down</i>	
<i>pecking at the ground</i>	<i>pecking at the ground</i>	<i>pecking into the ground</i>
<i>alarm call</i>	<i>alarm call</i>	<i>alarm call</i>
<i>attack call</i>	<i>plaintive charge call?</i>	"harsh scream"
<i>gakkering?</i>	<i>gakkering?</i>	
<i>hunched posture</i>	<i>hunched posture</i>	
<i>swoop and soar</i>	<i>swoop and soar</i>	<i>charge</i>
<i>bow</i>		
<i>quack</i>	<i>lateral head shakes</i>	<i>quick call</i>

rarely visit the outer parts of their territories except in search of food. Defence of the territories is limited mainly to the areas around the nests and roosting sites where the skuas spend their time when not foraging. They chase or display at any other skuas that intrude into these areas.

Because of the spacing of the nests and the lack of boundary disputes, most observations were made at the clubs where the non-breeding birds spend their time roosting, bathing and preening. They usually ignore each other but at times they are actively hostile. Their behaviour can be divided into two types. One is the reaction of a bird whose individual space is violated by another bird coming too close. It will either display and force the intruder to retreat or it will itself retreat. The other type is more complicated. A skua will walk towards another adopting an *upright posture* as it nears. Frequently, the approaching skua merely stops and relaxes or the other retreats a few yards, but at other times they circle each other in the *upright posture* (circular parading) and then sit side by side. Overt fighting is rare and short-lived. A skua may approach several others which are roosting in a group in this manner.

The circular parading is similar to that seen in the meeting ceremonies of mated birds, described by Moynihan (1962), so that it would appear these patterns are the preliminary stages of mating but, as it is impossible to distinguish the sexes, interpretation is difficult. Attempted copulation was seen only once in the course of this study, whereas Perdeck (1960) found it was

common in the clubs in the Shetland Islands. However, he also found that the skuas formed territories on the edges of the clubs where they paired but did not breed. If the Signy Island skuas formed such territories, they were of a very temporary nature, as the positions of the groups of birds in the clubs varied continually.

The skuas frequently fed in groups on dead penguins and seals. As at the clubs, there were cycles of activity. Several birds would feed together with very little aggression but the arrival of another bird would upset the *status quo* and displays would become more frequent until there was a continuous noise of *long calls*. If there was a fair number of birds intent on feeding, the effect was of a jostling to get at food. All the birds would be giving *obliques* but little notice would be taken of them except that one might retreat a little and try to get at the food from a different angle. If only a few birds were present, one would become dominant. This bird was often the occupant of an adjacent territory and it would spend so much time driving the other birds from the food that it had little chance to feed.

Description of behaviour patterns

Attack and escape behaviour. An attacking skua will rush at its opponent and peck at it, often grabbing feathers of the wing and tail. If the attacked bird fights back, both birds throw themselves forward and, jumping up, attempt to get on top of one another. The attack is delivered with the bill. The wings beat continuously to keep balance and to assist jumping, but they are not used as weapons as in other Lari, for example, the herring gull (*Larus argentatus*) (Tinbergen, 1953). These fights are short-lived and nothing was seen to compare with the prolonged fights of Dominican gulls (*Larus dominicanus*) at Signy Island, where the two birds would lock their bills and fight for several minutes. However, Clarke and others (1913) reported a fight between two brown skuas (*C.s. lönnbergi*) that lasted for 1 hour, after which the vanquished bird was so weak that it fell easy prey to a giant petrel (*Macronectes giganteus*). This appears to have been a territorial battle.

An attacked bird will often attempt to escape by running or flying. In some cases it appears that the escape drive is counteracted by another influence, for instance, it may try to get near food. Then, it will run around trying to avoid its opponent, while uttering low-pitched squeals. If caught by the attacker, the bird will emit harsh squawks or squeals similar to those of chicks that are being handled.

Re-directed attack behaviour. This form of behaviour was rarely seen, mainly because prolonged boundary disputes, where such behaviour is common in other skua populations (e.g. Stonehouse, 1956), were never seen at Signy Island. In conflict situations, where attack and escape drives appeared to be nearly equal, skuas often pecked at the ground or at the snow. Very rarely they would tear out lumps of moss with the bill and throw it sideways over the "shoulder" with a flick of the bill. This is the sideways nest-building movement of skuas and gulls. It is seen frequently after a skua has been relieved at the nest (for a detailed description of this, see Young (1963)). Moynihan (1962) found that *C.s. chilensis* did not drop material over its "shoulder" after tearing it out of the ground, but otherwise the action is widespread throughout the great skua's range. It occurs in *C.s. maccormicki*, although sideways throwing is not used in nest-building.

Grass-pulling was never seen, although Stonehouse described it for *C.s. lönnbergi* at South Georgia. This is not merely due to the small amount of grass in the South Orkney Islands, as the Dominican gulls will pull violently at a solid substrate, for example, the planks of a jetty. *Pecking at the ground* might be a low-intensity form of grass-pulling which was not seen because of the absence of high-intensity territorial disputes.

Re-directed attacks on other skuas were sometimes seen in feeding groups when a skua which had been attacked by another would retreat and then attack a third.

Displays

Upright. This posture (Fig. 1a) is often difficult to distinguish from that of a skua merely looking alert with neck stretched up, but the rounded appearance of the breast and the stiff-legged gait allow identification. The *anxiety upright* of *C.s. chilensis* and *C.s. skua*, as illustrated by Moynihan (1962) and Perdeck (1960), is absent in *C.s. lönnbergi*. In some *uprights* the neck may

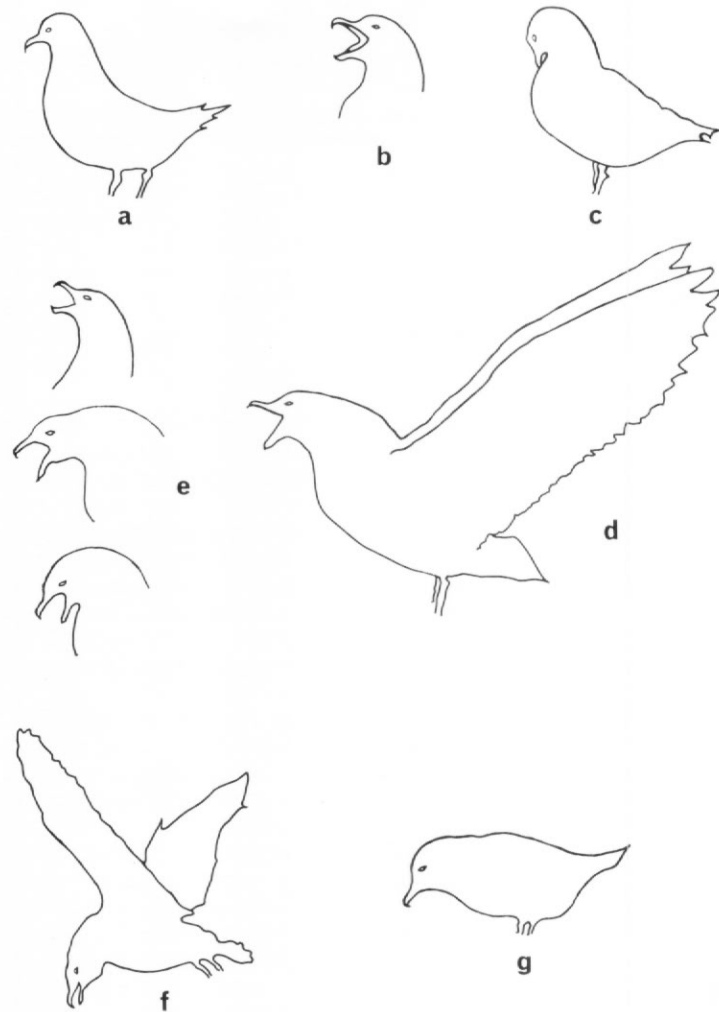


Fig. 1. Some displays of the brown skua, taken from still and ciné films. a. *Upright*; b. *Gape*; c. *Bent neck*; d. *Normal oblique*; e. *High, low and very low variants of the oblique*; f. *Aerial oblique*; g. *Hunched*.

be bent sideways or withdrawn so that the head is held away from the opponent. These forms are less aggressive than the normal one but they are still threatening and may precede an attack on the opponent. Sometimes when two skuas are circling each other in the *upright*, one may have its neck shortened. This also appears to be less aggressive. In the analysis of displays no distinction is made between the different forms of the *uprights*.

Both *C.s. skua* and *C.s. lönnerbergi* of the South Orkney Islands differ from *C.s. chilensis* and *C.s. lönnerbergi* of South Georgia (Stonehouse, 1956) in that the carpal joints are not held out from the body. Tinbergen (1959) suggested that the raising of the carpal joints is an intention movement of fighting with the wings. Although fighting with the wings is absent in those skuas that do not raise the carpal joints (which supports the theory), it is also absent in those that do. The only time that I saw raising of the carpal joints was when I was standing near a nest. The defending skuas would stand near me with wings held slightly out and at my slightest movement they would throw themselves into the air and attack. Here the raising of the carpal joints

was an intention movement of flying. Tinbergen has considered that pointing the bill downwards is also an intention movement of attack, and Moynihan (1962) has correlated the relative aggressiveness of the *anxiety uprights* of *C.s. chilensis* with the frequency with which it performs upward jabbing movements. In *C.s. lönnerbergi* the bill was sometimes pointed down in the less aggressive form of the *upright* but it was also pointed down more conspicuously immediately before the bird attacked, where downward jabbing is used. It is probably rash to correlate the form of the *upright* too closely with attacking movements as the bill is pointed down in the *approach posture* (equivalent to *upright*) of the Arctic tern (*Sterna paradisaea*), although this species does not downward jab (Cullen, 1956). On the other hand, terns, supposedly derived from gull-like ancestors, might have lost the mode of fighting but have retained it in ritual postures.

Oblique with long call (Fig. 2). This has been described in detail by Moynihan (1962). One feature not mentioned by him is the raising and lowering of the tail in time to the notes of the *long call*.



Fig. 2. *Obliques with long calls* being given by a pair as one lands by the other.

The *oblique* (Fig. 1d) can be divided into several variants: *without wing raising*, *high*, *normal*, *low* and *very low* (Fig. 1e). The last four are based on the posture of the neck during the display and they are normally well-defined distinctions, but the posture of the neck may vary during a display without any apparent change in stimulus situation. Also, a skua will follow the movements of an opponent by moving its neck. In such cases it was my procedure to record a display for analysis under the heading of the first variant assumed. As some variants are relatively rare, they have been combined into two groups for analysis: *low obliques* consisting of *low* and *very low obliques* and *obliques* comprising the rest.

Bent neck (Fig. 1c). As a reaction to another bird coming too close, a skua will stretch its neck up and bring the bill down to touch the breast feathers. This posture is held for a short time but it may be repeated several times in quick succession. Occasionally the full posture is preceded by several downward flicks of the bill. Sometimes these flicks may be seen without

the full posture following. They appear to be intention movements produced by a low level of motivation. The bill may be pressed very firmly into the breast feathers and, while there, preening movements may take place. Here, the lowering of the bill into the breast feathers appears to be a "transitional action" (Lind, 1959), an action common to both the display and preening, which triggers further movements of the latter activity. Sometimes the neck is held horizontally rather than vertically, so that the neck and body are in a straight line with the bill pressed against the breast pointing backwards.

A *bent neck* may be accompanied by *stifled long call notes*. The bill comes away from the neck as each note is uttered and the stifling could be due to a constriction caused by the position of head and neck. These notes are probably the same as the *rusty squeaks* described by Moynihan (1962).

Gape (Fig. 1b). At a very early age a skua chick will *gape*, that is, open its beak, at a human hand. Skuas will also *gape* at over-flying Antarctic terns (*Sterna vittata*). This suggests that the *gape* may be derived from an intention movement of pecking and is only slightly ritualized. There are two variants of the *gape*. A skua threatening another will give an *aggressive gape*, lunging forward, almost jabbing its opponent, but when threatened by another, a *defensive gape* with neck withdrawn will be employed.

Hunched posture (Fig. 1g). A skua may approach another which is feeding at a seal carcass, with its head lowered and neck withdrawn. If the skua is about to be attacked from the air it will freeze into this posture. The posture is also adopted both by chicks and by females when begging for food. Quacks (see below) or a soft, low-pitched call often accompany the posture, especially if the skua is being chased.

Bow. This display has not been recorded by other authors and it was rarely observed in this study. The skua adopts a posture very similar to the *food-begging low oblique* of the female (Moynihan, 1962). At the same time, it approaches or circles another skua with a stiff-legged gait like that seen in the *upright*. Sometimes the head is held away from the opponent as in the *upright*. Little can be said about the motivation of this display but it is certainly intimidating.

Quack. This is a quiet call denoting "uneasiness", as described by Stonehouse (1956). It is most frequently heard when a human intruder is in the territory but not near enough to the nest to precipitate *alarm calls* (see below). It is also produced by skuas standing near others which are feeding, apparently wanting to join the feeding group but afraid to do so.

Gakking. Moynihan (1962) heard calls consisting of a series of rapidly repeated, short emphatic notes that he suggested may be similar to the *gakking* of gulls. I heard this call a few times at Signy Island. On every occasion it was produced by a skua that was pursuing another in the air.

Alarm calls. *Alarm calls* are given by a skua when a potential predator approaches its brood. They are also given by a skua when its mate is trapped or shot. Only on one occasion was the *alarm call* heard outside a territory, when a skua, standing near a group feeding on a seal carcass, called several times for no apparent reason. Some of the other skuas looked alert but otherwise no notice was taken of it. When a non-breeding skua is trapped or shot, there are no *alarm calls* from other skuas as there are with mated birds; instead it is likely to be attacked.

This call is the equivalent of the *nest alarm call* described by Stonehouse (1956). Moynihan (1962) considered this was different from his *alarm long call notes*, but both authors described them as occurring when a human approaches the nest. Moynihan described *alarm long call notes* as being "single notes like abbreviated, somewhat sharper, versions of ordinary *long call notes*" and difficult to distinguish from the latter. As far as *C.s. lönnerbergi* is concerned, *alarm calls* and *long calls* are very different, the former being drawn out and plaintive. The calls of *C.s. antarctica* in the Falkland Islands appeared to me to be different from those of *C.s. lönnerbergi*, and P. J. Tilbrook (personal communication) suggests that the calls of *C.s. maccormicki* at the Argentine Islands also differ. Although direct comparisons have not been made (e.g. from tape recordings), geographical variation could account for differences between the descriptions of Moynihan's *alarm long call notes* and the *alarm calls* described above and by Stonehouse (1956).

Attack calls. These are uttered by skuas when attacking human intruders and they are similar to *alarm calls* but less plaintive. When a human approaches a skua on its nest, the

alarm call changes to the *attack call* as the skua leaves the nest and attacks. These calls may be homologous to the *plaintive charge calls* of gulls.

Swoop and soar. A skua will fly down at an intruder on the ground in its territory but, instead of landing and fighting, it glides past perhaps hitting with wings or feet, and soars up to repeat the manoeuvre. This pattern is directed against skuas, men, dogs and penguins. The infrequency with which this pattern leads to actual attack indicates that escape tendency is inhibiting the attack tendency. However, as Manley (1960) has pointed out, the *soar* may in part be due to the impetus gained by the *swoop* (Fig. 3). Re-directed *swoops* and those occurring *in vacuo* that Manley observed in the black-headed gull (*Larus ridibundus*) were never seen, neither were they used in a sexual context. It is likely, then, that the *swoops* and *soars* of skuas are not very ritualized.



Fig. 3. Skua swooping at an intruder near its nest.

Summary. The glossary (Table I) compares displays recognized by Moynihan, Perdeck and the present author. Only an approximate comparison can be made, because Moynihan (whose system has been followed here) gave a descriptive name to a whole display, whereas Perdeck named various morphological components of displays and combined them to describe any one display. Thus Moynihan's *very low oblique* is equivalent to Perdeck's *bend* (referring to the way the neck is held) *with wing raising*.

Differences between the three lists might be due to the length of each study, emphasis on different aspects and to what was considered as a display. With the exception of *gaping*, the differences lie mainly in the rarer displays and might therefore not be real. I saw the *bow* only six times in 2 years, and the *quack* is a very quiet call only likely to be heard if one is standing close to a skua in its territory. The lack of an *anxiety upright* in *C.s. lönnbergi* appears to be a real difference. It is surprising that this display, which is found in many of the Laridae

TABLE II. AGONISTIC DISPLAYS PERFORMED BY SKUAS IN THE CLUBS

	<i>Uprights</i>	<i>Gapes</i>	<i>Obliques without wing raising</i>	<i>High and normal obliques</i>	<i>Low obliques</i>	<i>Very low obliques</i>	<i>Bent necks</i>	<i>Bill downs</i>	<i>Pecking at the ground</i>	<i>Total number of displays in different situations</i>
Displays not in conjunction with overt attack or escape	196 (23)	134 (16)	22	164 (19)	2	—	12	1	—	531 (63)
Displays by attacker causing retreat	89 (13)	13	2	16	—	—	1	—	—	121 (14)
Displays by attacker before or during attack	23	9	2	14	—	—	—	—	—	48 (5)
Displays by attacker between successive attacks	—	—	2	—	1	—	—	—	—	3
Displays by attacker after attacks	1	2	2	21	5	1	—	—	—	32
Displays by attacked bird before being attacked	11	5	3	4	—	—	—	—	—	23
Displays by attacked bird after being attacked	2	9	3	19	—	1	—	—	—	28
Displays by attacked bird before or during escape	19	16	2	8	—	1	—	—	—	46 (5)
Displays by attacked bird after escape	—	—	—	1	—	—	—	—	—	1
Displays in conjunction with either overt attack or escape	145 (17)	54 (6)	16	89 (10)	6	3	1	—	—	308 (37)
TOTAL NUMBER OF DISPLAYS	341 (41)	188 (22)	38 (5)	247 (29)	8	3	13	1	—	839 (100)

Figures in brackets are percentages of the total number of displays in the table, rounded off to the nearest whole number. Percentages of five or less have been omitted.

TABLE III. AGONISTIC DISPLAYS PERFORMED BY SKUAS WHILE FEEDING IN GROUPS

	<i>Uprights</i>	<i>Gapes</i>	<i>Obliques without wing raising</i>	<i>High and normal obliques</i>	<i>Low obliques</i>	<i>Very low obliques</i>	<i>Bent necks</i>	<i>Bill downs</i>	<i>Pecking at the ground</i>	<i>Total number of displays in different situations</i>
Displays not in conjunction with overt attack or escape	12 (5)	13 (5)	13 (5)	52 (19)	6	—	20 (7)	1	10	136 (50)
Displays by attacker causing retreat	20 (7)	7	5	8	—	—	—	—	—	40 (14)
Displays by attacker before or during attack	8	1	—	8	—	—	—	—	—	11
Displays by attacker between successive attacks	—	—	—	2	1	—	—	—	—	3
Displays by attacker after attacks	—	2	1	32 (19)	10	4	—	1	1	51 (19)
Displays by attacked bird before being attacked	2	1	—	—	—	—	—	—	—	3
Displays by attacked bird after being attacked	—	3	—	6	1	—	—	—	—	10
Displays by attacked bird before or during escape	—	4	—	—	—	—	—	—	2	6
Displays by attacked bird after escape	—	—	—	2	1	—	—	—	—	3
Displays in conjunction with either overt attack or escape	30 (11)	18 (7)	6	58 (22)	13 (5)	4	—	1	3	153 (50)
TOTAL NUMBER OF DISPLAYS	42 (16)	31 (12)	19 (7)	110 (42)	19 (7)	13 (5)	20 (7)	2	13 (5)	269 (100)

Figures in brackets are percentages of the total number of displays in the table, rounded off to the nearest whole number. Percentages of five or less have been omitted.

TABLE IV. AGONISTIC DISPLAYS PERFORMED BY SKUAS ENGAGED IN INTRASPECIFIC TERRITORIAL DEFENCE

	<i>Uprights</i>	<i>Gapes</i>	<i>Obliques without wing raising</i>	<i>High and normal obliques</i>	<i>Low obliques</i>	<i>Very low obliques</i>	<i>Bent necks</i>	<i>Bill downs</i>	<i>Pecking at the ground</i>	<i>Total number of displays in different situations</i>
Displays not in conjunction with overt attack or escape	4	—	3	156 (53)	3	15 (5)	52 (18)	—	—	233 (79)
Displays by attacker causing retreat	3	—	1	2	—	—	1	—	—	7
Displays by attacker before or during attack	5	—	—	2	—	—	2	—	—	9
Displays by attacker between successive attacks	—	—	—	2	—	—	—	—	—	2
Displays by attacker after attacks	—	—	—	21 (7)	—	—	1	—	—	22 (7)
Displays by attacked bird before being attacked	2	—	—	3	—	—	2	—	—	7
Displays by attacked bird after being attacked	—	—	—	11	2	—	—	—	—	13
Displays by attacked bird before or during escape	—	—	—	1	—	—	—	—	—	1
Displays by attacked bird after escape	—	—	—	—	—	—	—	—	—	—
Displays in conjunction with either overt attack or escape	10	—	1	42 (14)	2	—	6	—	—	61 (21)
TOTAL NUMBER OF DISPLAYS	14 (5)	—	4	198 (67)	5	15 (5)	58 (20)	—	—	194 (100)

Figures in brackets are percentages of the total number of displays in the table, rounded off to the nearest whole number. Percentages of five or less have been omitted.

should be absent in *C.s. lönnerbergi* but present in the closely related *C.s. chilensis*. The other feature lacking from the displays of *C.s. lönnerbergi* is tail raising. This occurs in *uprights* and *bent necks* (*bends*) of *C.s. chilensis* and *C.s. skua*.*

ANALYSIS OF SOME DISPLAYS

Causation. Previous studies have shown that hostile displays are caused by conflicting attack and escape tendencies (Tinbergen, 1959). The relative levels of these tendencies can be deciphered by the time-score method of noting quick successions of displays and overt behaviour such as attack or escape. The method used by Moynihan (1962) on *C.s. chilensis* was repeated in this study to get a direct comparison between the subspecies, but with alterations to include more situations. The results of observations from December 1965 to March 1966 are shown in Tables II, III and IV, and they can be compared with those of Moynihan (1962). Apart from the inherent drawback to this method, that environmental factors affecting a bird's attack and escape tendencies are not constant, the results are not as significant as I had hoped because most displays took place without any recordable overt behaviour, and many types of display were seen only infrequently.

As described earlier (p. 15-17), the overall pattern of behaviour varies between territory occupiers, feeding groups and birds in clubs. This was reflected in the proportions of displays recorded, so observations of displays in the three categories have been kept separate. The relative levels of the tendencies of attack and escape can be examined by noting the frequencies of displays in relation to overt attack and escape as shown in Table V. Threatening birds will

TABLE V. DISPLAYS PERFORMED IN CONJUNCTION WITH OVERT BEHAVIOUR

	<i>Upright</i>	<i>Gape</i>	<i>Oblique</i>	<i>Low oblique</i>	<i>Bent neck</i>
By attacker before attack or causing retreat (threatening bird)	148	30	60	0	4
By attacker after being attacked or before or during retreat (threatened bird)	21	32	52	5	0

have a high proportion of attack tendency compared to escape tendency, and in threatened birds the proportion will usually be reversed (but not always, as an attacked bird may not retreat or may proceed to attack another bird).

The *upright* is the most aggressive display, having a small escape component in it. In the few boundary disputes seen, the upright was employed by the defending pair, causing the intruding pair to retire immediately. Only on two occasions has a threatened skua been seen to assume an *upright* after being attacked.

Either attack or escape may predominate in a *gape*, depending on whether it is an *aggressive* or *defensive gape*. It is a relatively defensive display yet it is intimidating, being seen when two birds come close together, and it prevents attack by the threatening skua or pursuit after attack.

The *obliques* occur when there is a near balance between the two tendencies. A feature of the feeding groups is that when the birds actually feeding are frequently adopting *oblique* postures, birds standing a short way off will also adopt *obliques*. Although they are neither

* During a stay on Foula in the Shetland Islands in June and July 1967 I made some observations on *C.s. skua* in order to compare my interpretation of their behaviour with that of Perdeck (1960), who studied the same population.

Although it was not possible to make a quantitative study, I was able to confirm that there were many differences between *C.s. skua* and *C.s. lönnerbergi*. On Foula, I found that the division of *uprights* into *aggressive* and *intimidated* varieties was very noticeable, as was the *quick call* accompanying the *intimidated upright*. Tail raising was frequently seen during *uprights*, as was the raising of the carpal joints which Perdeck did not report. I heard *quacks* but never saw any *gaping*. My observations were not complete so that I cannot comment on other calls and postures that Perdeck did not see.

threatening nor being threatened, their motivation is raised by the sight of the displaying feeders. In other words, the *obliques* seem to have an infectious quality, even at a distance, suggesting that the overall level of motivation for *obliques* is low. *Low obliques* are less aggressive than the other variants, being characteristic of birds being driven away from the feeding groups. Very frequently, birds which produced a *normal oblique* when threatened changed to a *low* or *very low oblique* as they retreated.

The *bent neck* is frequently used by the occupier of a territory when threatening an intruder on the ground and it is rarely followed by an attack, so the overall resultant of attack tendency will be low. It is unlikely that there is a high escape tendency as the bird giving the *bent neck* is in its own territory and *bent necks* were rarely recorded as being given by a skua when it was threatened.

The four displays discussed above are not merely caused by the skuas' tendency to attack and escape but also by the distance between the skua and its rival. It is reasonable to suggest, as Perdeck (1960) has done, that skuas flying overhead constitute a weaker stimulus than do skuas approaching or threatening on the ground, and that skuas faced by the latter situation are more likely to have a weak attack tendency, so any display they adopt would have a small attack component. This would be only a partial explanation of the observed differences in Table VI which shows displays directed at over-flying skuas, that is those at a distance, and

TABLE VI. DISPLAYS PERFORMED BY SKUAS IN REACTION TO TWO TYPES OF STIMULUS SITUATION

	Over-flying skuas	Skuas approaching or threatening on the ground
CLUB		
<i>Upright</i>	0	38 (23)
<i>Gape</i>	0	57 (35)
<i>Oblique</i>	4 (2)	57 (35)
<i>Bent neck</i>	3 (2)	4 (3)
Total	7 (4)	156 (96) = 163 (100)
FEEDING GROUP		
<i>Upright</i>	0	1 (2)
<i>Gape</i>	0	11 (17)
<i>Oblique</i>	17 (26)	22 (34)
<i>Bent neck</i>	12 (19)	1 (2)
Total	29 (45)	35 (55) = 64 (100)
TERRITORIES		
<i>Upright</i>	0	1 (1)
<i>Gape</i>	0	0
<i>Oblique</i>	110 (76)	3 (2)
<i>Bent neck</i>	23 (16)	7 (5)
Total	133 (92)	11 (8) = 144 (100)
TOTAL OF THE THREE CATEGORIES		
<i>Upright</i>	0	40 (11)
<i>Gape</i>	0	68 (18)
<i>Oblique</i>	131 (35)	82 (22)
<i>Bent neck</i>	38 (10)	12 (4)
Total	169 (45)	202 (55) = 371 (100)

Figures in brackets are percentages. Skuas approaching or threatening on the ground in territories were rarely observed.

displays directed at skuas approaching or threatening on the ground, that is those nearby. Although the former are weak stimuli and the latter strong, the displays they elicit also depend on the distance between the birds, and this depends on what situation the displaying bird is in.

Proportions of displays at over-flying skuas vary between the three categories due to the effect of ownership of an area. Non-territorial skuas defend the individual space which is 2 or 3 m. across in the clubs but it may be very much less in the feeding groups, whereas territory occupiers react to intruders over a vastly greater area including the air space above it. The explanation of the difference in the proportions of displays observed in each category of Table VI is that some displays, *uprights* and *gapes*, are directed at skuas a short distance away. *Bent necks* are directed either at over-flying skuas or at those more than 10 m. away on the ground; that is, they are directed at distant skuas (the relatively high percentage of *bent necks* in feeding groups is due to reactions of dominant skuas who are usually territory occupiers). The situation of *obliques* is more complicated. While they are used as long-distance advertisements by a skua in its territory, they are also used in non-territorial contexts by skuas quarrelling over food.

The two threatening displays not mentioned so far, the *bill down* and *pecking at the ground*, were seen too infrequently for quantitative analysis. The *bill down* is a momentary posture that may be repeated several times in quick succession. It may be an intention movement of *pecking at the ground* as they both occur in the same situations and appear to have the same motivation. They are most frequently seen when a skua has displayed at another but the latter has failed to retreat. The skua is relatively aggressive but it is inhibited from following up the attack. The *bill down* also occurs after a skua has been driven away from food. It stands nearby looking towards the food, apparently wanting to go back, but the presence of the other skua prevents it from doing so.

The motivation of these postures corresponds to some mixture of attack and fleeing, but in the *hunched posture* the skua has a fleeing motive that is counteracted by other tendencies such as an approach to a parent or mate for food, or an approach to food in the presence of other skuas. In these cases the posture is apparently one of appeasement.

Function. Postures of gulls have been divided into *distance increasing* and *distance reducing displays* (Tinbergen, 1959), the former tending to cause other birds to retreat from the displaying bird and the latter tending to allow the displaying bird to come near another. Stokes (1962) has shown that the great tit (*Parus major*) and the blue tit (*Parus caeruleus*) showed more escape and less attack behaviour in the presence of rivals in aggressive postures than in the presence of those showing escape behaviour. The aggressive displays of skuas have the same affect of eliciting escape behaviour from rivals (Table VII), showing that they have the function

TABLE VII. THE SIGNAL VALUES OF HOSTILE DISPLAYS

<i>Behaviour of bird</i>	<i>Reaction of rival</i>		
	<i>Stays</i>	<i>Attacks</i>	<i>Escapes</i>
<i>Upright</i>	44 (51)	18 (19)	100 (92)
<i>Gape</i>	12 (11)	6 (5)	21 (22)
<i>Oblique</i>	18 (15)	5 (6)	25 (27)
<i>Bent neck</i>	8 (4)	2 (1)	2 (7)

Figures in brackets are values calculated on the basis of "null hypothesis" that the different postures are equally likely to be followed by "stay", "attack" or "escape".

of signalling threat and so tend to space the birds (during these observations no record was kept of the reactions of rivals to fleeing behaviour). Although the figures in Table VII are rather small and no account has been taken of the rival skua's motivation before the display, they suggest that the different displays do not have significantly different effects on the rival (if this was so, Table VII would show a significant difference between the observed and calculated figures for each display). Thus, the communicative function of the displays is poorly developed on the receiving side and the presence of several threatening displays would seem to

be superfluous. At least, effectiveness of different degrees of threat has yet to be demonstrated in skuas, as it has been in the glaucous-winged gull (*Larus glaucescens*) by Stout and Wilcox (1966).

The only unequivocal *distance reducing display* in the skua repertoire is the *hunched posture*. It is very similar, morphologically, to the *hunched posture* of gulls and appears to have the same function. It allows one skua to come near another which would attack it in other circumstances, as in feeding groups where a skua approaching the dominant skua in the *hunched posture* could come alongside it and feed, but one approaching "confidently" with neck stretched up would be attacked. This also seems to be the case with both chicks and females begging for food in the posture.

Comparison with the displays of gulls. Comparison of the skuas (Stercorariinae) and the gulls (Larinae) is rather difficult as few species have been studied in detail, and results from different studies on the same species may vary (as in those on *C. skua*). Furthermore, no behaviour pattern has been fully analysed. Several features on the behaviour of skuas and gulls are similar; for instance, both sexes participate in nest-building, incubation and care of the young, and the multiple cloacal contacts during copulation are a unique feature of all Laridae (Tinbergen, 1963). There are also many agonistic patterns to be found throughout the Laridae, including *upright*, *oblique*, *peck at ground*, *hunched*, and the various alarm and attack patterns. Examining the occurrence of some displays in various species of Stercorariinae and Larinae as shown in Table VIII, it is noticeable that the agonistic *choking* is wholly absent from the repertoire of the Stercorariinae and the appeasing *head-tossing* and *head-flagging* are rare.

Tinbergen (1959) suggested that *choking* is derived from the depositing of material in the nest, an action not performed by the Stercorariinae, thus explaining their lack of *choking*. The occurrence of *head-tossing* and *head-flagging* in the Stercorariinae is hard to define. Perdeck (1963) has stated "when pecking from below [in food begging], the female [Arctic skua] may make short upward movements reminiscent to the *head-tossing of gulls*" [*sic*]. He also noted such movements in the food begging of *C. skua* (Perdeck, 1960). I have never observed these movements in *C.s. lönnerbergi* but Moynihan (1962) noted that some of the pecks delivered by the female of *C.s. chilensis* were "directed more strongly upwards than others, and some of these were slightly reminiscent of the lowest intensity *head-tossing* movements of gulls". He concluded "They were almost certainly no more than ordinary pecking movements with slightly unusual orientation". Thus it would seem that apparent *head-tossing* movements in *S. parasiticus* and *C. skua* may be no more than jabs of the bill that are directed upwards because the female is in the *hunched* or *food-begging low oblique postures*, and may be intention movements of actual pecking rather than of escape that have given rise to *head-tossing* in gulls. *Head-flagging* in gulls is apparently motivated by the escape drive and the *head-flagging* movements observed by Moynihan (1962) and Stonehouse (1956) may well be unritualized intention movements of escape. The *head-flagging* of *S. longicaudus* (Drury, 1960) seems to be a well-defined ritualized pattern.

The absence or reduction of ritualization in the Stercorariinae of certain patterns that are present in the Larinae can be correlated with a greater incidence of overt attack and escape in the former. This could be due to taxonomic differences, as the Stercorariinae are presumed to have been derived from a gull-like ancestor and may have diverged when only some displays had arisen, but this only explains differences in the display repertoire and not the lack of displays covering the same situation as those of gulls. An aggressive skua is not prevented from attacking by the display of its rival, except in the case of the rather rare *hunched posture*, and, as there is no equivalent of *choking* conveying "Don't attack, if he is attacked he will fight back" (Tinbergen, 1959), there is no display to take the place of overt attack or escape when there is a high-level conflict between attack and escape tendencies. If the Stercorariinae and Larinae had been exposed to the same environmental pressures, it would be reasonable to suppose that equivalent, although not necessarily similar, displays would have been evolved, as had been suggested by Moynihan (1960). Parallel evolution of this sort has occurred between the Larinae and Sterninae, the latter also supposedly derived from a gull-like ancestor. For instance, the *tilting* of the black-capped terns is equivalent to the *head-flagging* of gulls (Cullen, 1956). One difference in environment that could account for the difference in evolution of displays is nesting density. The Stercorariinae nest in relatively large territories but most

TABLE VIII. DISPLAYS AND NEST DENSITIES OF STERCORARIINAE AND SOME LARINAE

Species	Displays					Nest density	Authority
	Upright	Oblique	Choking	Head-tossing	Head-flagging		
STERCORARIINAE							
Great skua (<i>Catharacta skua</i>)	×	×				Low	
Arctic skua (<i>Stercorarius parasiticus</i>)	×	×				Low	Perdeck (1963)
Long-tailed skua (<i>S. longicaudus</i>)	×	×			×	Low	Drury (1960)
Pomarine skua (<i>S. pomarinus</i>)		×				Low	Pitelka and others (1955)
LARINAE							
Hemprich's gull (<i>Larus hemprichi</i>)	×	×	×	×	×	Low	Fogden (1964)
Sabine's gull (<i>Xema sabini</i>)	×	×	×	×	×	Low	Brown and others (1967)
Black-headed gull (<i>L. ridibundus</i>)	×	×	×	×	×	High	Moynihan (1955)
Grey gull (<i>L. modestus</i>)	×	×	×	×	×	High	Moynihan (1962)
Herring gull (<i>L. argentatus</i>)	×	×	×	×	×	High	Tinbergen (1953)
Common gull (<i>L. canus</i>)	×	×	×	×	×	High	Weidmann (1955)
Laughing gull (<i>L. atricilla</i>)	×	×	×	×	×	High	Noble and Wurm (1943)
Dophin gull (<i>L. scoresbii</i>)	×	×		×	×	High	Moynihan (1962)
Ivory gull (<i>L. eburneus</i>)	?	×	×	×	×	High	Bateson and Plowright (1959)
Hartlaub's gull (<i>L. novae-hollandiae</i>)	×	×	×		×	High	Tinbergen and Broekhuysen (1954)
Little gull (<i>L. minutus</i>)	×	×		×	×	High	Moynihan (1955)

* The little gull has the equivalent *tilting*.

of the Larinae and Sterninae nest in colonies, and therefore have only small territories. As nesting density increases, there will be a rise in aggression for birds will be more likely to come into conflict with neighbours, as Palmer (1941) found in the common tern (*Sterna hirundo*), and when nest density is high (due to some other pressure) there will be pressure to reduce the overt aggressive behaviour that would otherwise disrupt the colony. This appears to have happened in the weaver birds (Ploceinae) where grain-eating species nest in colonies and insect-eaters live in open territories. The aggressive behaviour of the colonial species is of a static type, consisting of displays, whereas that of species with open territories consists of chasing (Crook, 1964).

The lack of appeasement displays in the meeting ceremonies of Stercorariinae may also be related to spacing out. The few, often unritualized, patterns found in some Stercorariinae are to be contrasted with the well-developed, appeasing *head-flagging*, *head-tossing*, *upward choking* and *tilting* in the meeting ceremonies of other Laridae. A bird returning to its nest in a colony will have more "need to appease" its mate as the latter will have a higher level of aggression, due to the proximity of its neighbours, than if it was in comparative isolation.

It is difficult to correlate high nest density with extensive ritualization of aggressive behaviour in the Laridae, as frequently there is no information available on nest density, which may vary in different localities anyway (as it does in various populations of *C. skua*). Support for a possible correlation is given by the fairy tern (*Gygis alba*) which is less gregarious than most Larids and has fewer hostile patterns (Dorward, 1963). Table VIII shows that, in general, the Stercorariinae have widely spaced nests and few displays, whereas Larinae nest in colonies and have more displays, but there are two exceptions listed under Larinae. Hemprich's gull (*Larus hemprichi*) and Sabine's gull (*Xema sabini*) both nest relatively solitarily yet they have the full complement of displays. If it can be accepted that the spacing of the nests of these two gulls was caused by some change in environment after the displays had evolved, then it is possible to conclude that the Stercorariinae became widely spaced nesters early in their evolution from the gull-like ancestor, and that there has not been the same pressure for ritualization of hostile behaviour as there was in the Larinae.

DEFENCE OF TERRITORY AND BROOD

Defence against other skuas

As mentioned on p. 15, boundary disputes are rare, territory owners only reacting to intruders within the boundary area of the territories if they themselves were there. Patterson (1965) has shown in black-headed gulls that it is distance from the owner that determines whether an intruder is attacked or not and this is probably the case in skuas, except that a skua may fly several hundred yards to drive out intruders if they are in a penguin rookery that is part of its territory. As the skuas spend most of their time in a small area surrounding the nest or on nearby roosting sites, defence is concentrated there. Over-flying skuas are displayed at or chased and any skua that lands in this area is promptly attacked and driven out.

Quantitative recording of variations in response to intruders throughout the season was not attempted, but defence was seen to start as soon as the birds took up their territories in October and to continue until they left in March. There was no obvious difference in response between the periods with and without eggs or young, but defence was more vigorous when territories were first established, and were weaker at the end of the season when the young were flying.

The reactions to intruding skuas can be regarded either as defence of the breeding area, thus spacing the breeding population, or as defence of the brood from potential predators or both. Young (1963) found that *C.s. macconnicki* only reacted to over-flying intruders that circled over the territory. This circling flight is characteristic of a hunting skua, so these skuas were reacting to potential predators in much the same way as Kruuk (1964) found that black-headed gulls reacted to herring gulls when they started to stall. I observed a more positive indication that intruding skuas are regarded as potential predators when a skua displayed at an over-flying skua, ran to its chick and stood looking alert until the intruder had gone, but as this was the only time I saw such active protection, and as I have seen skuas ignore the squeals of juveniles being attacked by other skuas, territorial defence seems to be the main cause of reaction.

TABLE IX. THE RESPONSE OF THREE BREEDING PAIRS TO INTRUDING SKUAS FLYING OVER THE TERRITORY

	<i>Behaviour of intruder</i>	
	<i>Fast flight</i>	<i>Slow flight</i>
Response	58	71
No response	30	35
Total	88	106
Percentage response	66	67

The absence of *alarm calls*, elicited by other potential predators, also suggests that intruding skuas are regarded mainly as violators of the territory. This is shown by the observations on the responses of three pairs of skuas to over-flying skuas in Table IX. *Slow flight* refers to the meandering, often circling, flight of a hunting skua and *fast flight* to rapid flying in a straight line. Responses consist of displays, *obliques* or, rarely, *bent necks* and chases. The results, based on 194 observations, show no difference between response to skuas showing hunting behaviour and those merely invading the territory. At Signy Island predation by skuas on skua broods appears to be very small (Burton, 1968), but in other populations it is substantial (Young, 1963) and the reactions of skuas to intruders may be different.

Defence against other species

Giant petrels (*Macronectes giganteus*) and sheathbills (*Chionis alba*), which are known to take the broods of other species, are unlikely to take the broods of skuas. The former are too ungainly on the ground to catch the very mobile skua chicks, and only one skua nest on Signy Island is within the territory of a sheathbill. There remain only "potential predators", seals and penguins which may wander near skua broods, but they are unlikely to harm them except by accident, and Man, who is undoubtedly a predator of skua adults and broods in some places, has rarely killed them on Signy Island.

There is no information about skuas' reactions to the giant petrel and sheathbill when on the ground in a skua's territory, but they are ignored when flying overhead. On Signy Island, fur seals (*Arctocephalus tropicalis*) sometimes wander quite close to skua nests but without any reaction from the skuas. Penguins may evoke response, as when groups of Adélie penguins (*Pygoscelis adeliae*) wander through the skua territories the parent skua will run over and stand between them and the chicks. If the penguins come too close to the chicks, the skua will utter *alarm calls*, hover over and perhaps *swoop* at them. On one occasion a group of penguins found a skua nest in their path. The skua that was incubating gave *alarm calls* and two of the penguins walked forward and drove it off the nest. The skua continued calling and slowly advanced back to its nest and sat on it. After a few minutes the penguins withdrew. On this and on other occasions the mate of the skua which was giving the *alarm calls* took no action against the penguins but merely looked alert.

Defence against Man

Buzz, alarm call, attack call, swoop and soar, and hover. As the intruder enters a territory, a skua will fly down from the roosting site, glide over the intruder and fly back. This is the *buzz* and may be repeated two or three times. The *buzz* may be observed at least a week prior to egg-laying. Weakly aggressive skuas often *hover* just above and behind the intruder, rather than *swoop* and *soar*. This pattern is also directed against penguins. *Attack calls* are uttered at the same time.

As the intruder approaches the brood the reaction becomes stronger. *Buzzing* is replaced by *swoops* and *soars* which are initially weak with the skua often landing between successive attacks. Nearer the nest the *swoops* become more vigorous and the *attack calls* more frenzied.

Measurements of the rate of *swooping* (Table X) were made at three nests during February when the chicks had left the immediate nest area. During this month *swooping* is at its greatest but it is difficult to record as non-breeding skuas are attracted to the disturbance and the defending pair break off attacking the human intruder to chase off the other skuas. The change in rate of attack is due to alteration of the form of attack. At a distance from the brood, the skuas circle round the intruder between each *soar* and *swoop*. As the brood is approached, the circling is omitted, and the skuas "stall turn" at the top of each *soar*.

TABLE X. INCREASE IN RATE OF SWOOPING AS A HUMAN INTRUDER APPROACHES THE NEST

Nest number	Number of tests	Individual skuas	Mean swoops per minute at fixed distances from the brood		
			40 m.	20 m.	0 m.
44	7	Mauve/Blue	1.7	4.6	8.8
		Unringed	1.7	6.4	9.4
46	10	Red/White/Green	2.9	3.1	4.9
		Blue/Yellow	1.7	4.4	5.8
49	7	Yellow/Green	—	3.3	11.2
		Blue/Black	—	3.7	9.9

These observations show that a man represents an increasing stimulus for anti-predator reactions as he approaches a skua nest. The threshold at which the various components of the reaction are evoked will be determined by the resultant of internal and other external factors, and will be inversely related to the distance of the intruder from the nest, i.e. if he is attacked a long way from the nest, the threshold is low. This was used as the basis of an experiment to show seasonal variation and to relate short-term changes to various external factors, for if all factors affecting threshold of responses except one are kept constant, then changes in the one will be reflected in the distances from the nest at which the reaction is elicited. In seven territories, stakes were placed at 10 yd. (9.1 m.) intervals in a line leading up to the nest and I walked along them at a constant speed noting how far I was from nest or chicks when a certain reaction was elicited. This could only be done in territories on flat ground where a skua sitting on the nest was able to see the intruder as soon as he entered the territory. To keep the stimulus as constant as possible from one test to another, I always wore the same colour clothing and held a ski-stick above my head (to ward off attacks). During the incubation periods, tests were carried out up to three times a day, but later they were performed less frequently. When the chicks moved from the nests, the stakes were moved to line up with their resting places or the measurements were adjusted after the test. Tests were started shortly after the first eggs were laid. Prior to this there are no anti-predator reactions except *buzzing* by some birds.

Immediate factors affecting reactions to Man

Physical factors. Initially it was suspected that some aspects of weather would affect the strength of the anti-predator reactions. Baerends (1959) found that in adverse weather the tendency of a herring gull to sit on its eggs is so great that it is very reluctant to rise and retrieve an egg from the nest rim. It is reasonable to suppose that this tendency could also conflict with anti-predator reactions, but it was not possible to demonstrate this in the brown skua as air temperature during the incubation period ranged only a few degrees either side of freezing point. Incident radiation and wind were more likely to influence incubation behaviour, and so anti-predator reactions, but extremes of these factors were too rare for a study to be made. Wind did affect the *swoop* and *soar* attacks because skuas can fly more easily in a high wind, but again it was not possible to investigate this. Skuas sat firmly on the nest if partly buried in drift snow but this may have been due to the difficulty of forcing their way out rather than to any increase in incubation tendency.

Biotic factors. The data from the tests were examined by pairing observations in which a certain environmental factor differed, for example, partner present or absent. By taking a "before and after" average for one situation, differences between the two situations due to a seasonal variation in response or to habituation were kept to a minimum. This was difficult in practice as both skuas might be present several tests running, and at some nests one of the skuas was rarely on the nest when a test was made. For this reason the number of pairs of observations was usually too small for a test of significance but, as each skua showed the same trend, results were combined and a sign test was used in comparing changes in response.

Example:

Date 1966	Distance from nest (yd.)	Behaviour of skuas
16 January	45	Yellow/Yellow calls on ground
	40	Red/Red calls on ground
	20	Both attack
17 January	60	Yellow/Yellow calls on ground
	30	Yellow/Yellow attacks Red/Red absent
18 January	50	Yellow/Yellow calls on ground
	40	Red/Red calls on ground
	15	Yellow/Yellow attacks
	10	Red/Red attacks

For Yellow/Yellow attacking: when Red/Red absent, distance = 30 yd.
when Red/Red present, distance = $(20+15)/2 = 17.5$ yd.
For Yellow/Yellow calling: when Red/Red absent, distance = 60 yd.
when Red/Red present, distance = $(50+45)/2 = 47.5$ yd.

Here, Yellow/Yellow attacks and calls when the intruder is a greater distance from the nest and when Red/Red is absent from the territory. Similar comparisons were made throughout the season for all factors.

Incubating or brooding. The "on duty" parent (the skua sitting on the nest) would start to give *alarm calls* earlier than if "off duty" ($N = 61, p < 0.001$). After leaving the nest as the intruder approaches, the "on duty" parent stands calling and only attacks when the intruder is much nearer than if it is "off duty" ($N = 46, p < 0.001$), showing that brooding tendency is in conflict with attacking. This is the opposite to the response of waders, in which Simmons (1955) found that anti-predator reactions are more vigorous when the brooding is intense.

Absence of mate. The behaviour of a skua is significantly different when its mate is absent. It has a lower threshold for *alarm calls* ($N = 109, p = < 0.001$), which recall the mate immediately if it is within earshot. An increased tendency to sit on the nest when the mate is absent ($N = 150, p = 0.008$) is difficult to understand. Such a reaction would be of value if the intruder was a predator of the brood only, as any value incurred by the cryptically coloured adult sitting on the brood is lost by the *alarm call* informing the predator that there is a nest there. Similarly, there is no reasonable explanation for the increased tendency to attack when the mate is absent ($N = 112, p = < 0.001$) which is less marked during the incubation period due to the conflict between attack and brooding tendencies.

Long-term factors affecting reactions to Man

By averaging the results of tests over periods of 12 days to remove the effects of the immediate factors discussed above, the seasonal variation of response can be demonstrated. Habituation to the stimulus of a human intruder was, if anything, slight as was shown by the seasonal variation being similar at nests that were visited only infrequently.

Although individuals vary, there is an overall trend which is shown in Figs. 4 and 5. Attacks are absent or very weak for the first few days after the eggs are laid. Some skuas continue to attack weakly until the chicks hatch, when there is a sharp rise. The attacks of others increase progressively with no special increase after their chicks hatch. Attacks of most birds reach a peak before the chicks start to fly, after which there is a decrease. After the chicks had fledged, it was difficult to make tests because both of the adults were often absent at the same time and the chicks ran around or were hard to find. Testing had to be abandoned when the juveniles could fly well as there was no point of reference for the measurements. At about this time the intensity and rate of attacks, which could not be measured in these tests, decreased sharply. Often the attacks died out despite an increasing stimulus in the form of the intruder approaching the young. This partly explains the increase at the end of the season (Figs. 4 and 5), when the adults flew out to me when I was a long way from the young but they only attacked a few times before landing again.

It can be seen that the two birds of a pair tend to follow the same pattern of response. It usually happened that the more aggressive bird in each pair would start the attacks and the other would follow it, its response apparently being facilitated by the first bird's behaviour. The different levels of response between the two birds of a pair were not related to sex but to inherent levels of aggressiveness. For instance, in 1964-65 Mauve/Green (a male) was more aggressive than its mate. The next year Mauve/Green mated with Blue, an established breeder who had been less aggressive than her previous mate. Of this new pair Blue was the more aggressive.

Seasonal variations in motivation of *alarm calls* follows the same trend as that of attacks (Figs. 4 and 5), but there is a difference at the beginning of the season. Unlike attacks, *alarm calls* are heard as soon as eggs are laid, at least in the majority of birds. Also, some birds show a very high level of response at the start of the season. From the few individuals tested, it was not possible to discern any other behaviour that could be correlated with this.

Discussion

Causal aspects. Skuas reactions to other skuas have a spacing out effect on the individual birds, at least other than mates, and perhaps they result in the spacing out of the breeding population as well. The reactions to other potential predators are to defend the brood. When intruding skuas followed me into a territory, the defending pair only attacked them half-heartedly, concentrating the bulk of their attacks on me. These attacks continued until I had retreated well beyond the intruding skuas. This subservience of intraspecific aggression to anti-predator response has also been found in waders (Simmons, 1955).

Other parts of parental behaviour, for example, nest building and incubation, have been shown to be controlled by hormones (Lehrman, 1961), and it seems likely that control of anti-predator behaviour in skuas is also hormonal, as Vowles and Harwood (1966) have demonstrated in ring doves (*Streptopelia risoria*). The reactions of doves differed from those of skuas in that a peak of response was attained as the eggs were laid, with a secondary peak on hatching but there was a similar decline as the chicks became independent. Vowles and Harwood showed that injections of prolactin and progesterone increased defensive response to a predator. Anti-predator behaviour differs from other components of parental behaviour in that it occurs throughout the breeding period from the time that the eggs are laid (if not before) to the time that the juveniles can fly.

Hormonal factors are initiated and maintained by external stimuli. Presence of the brood must be the most important of these, although subsidiary factors such as presence or absence of the mate cause fluctuations of the response. Response develops quickly, appearing as soon as the eggs are laid. This could be due to a build-up of motivation caused by courtship, nest-building, etc. If the eggs are lost shortly after being laid, anti-predator reactions that are weak at that stage disappear immediately but, if eggs or young are lost later in the season, the reactions will continue for a day or two. This suggests that there is some central control of defence of the brood which is initiated and maintained by stimuli from the brood and which persists after the stimuli disappear.

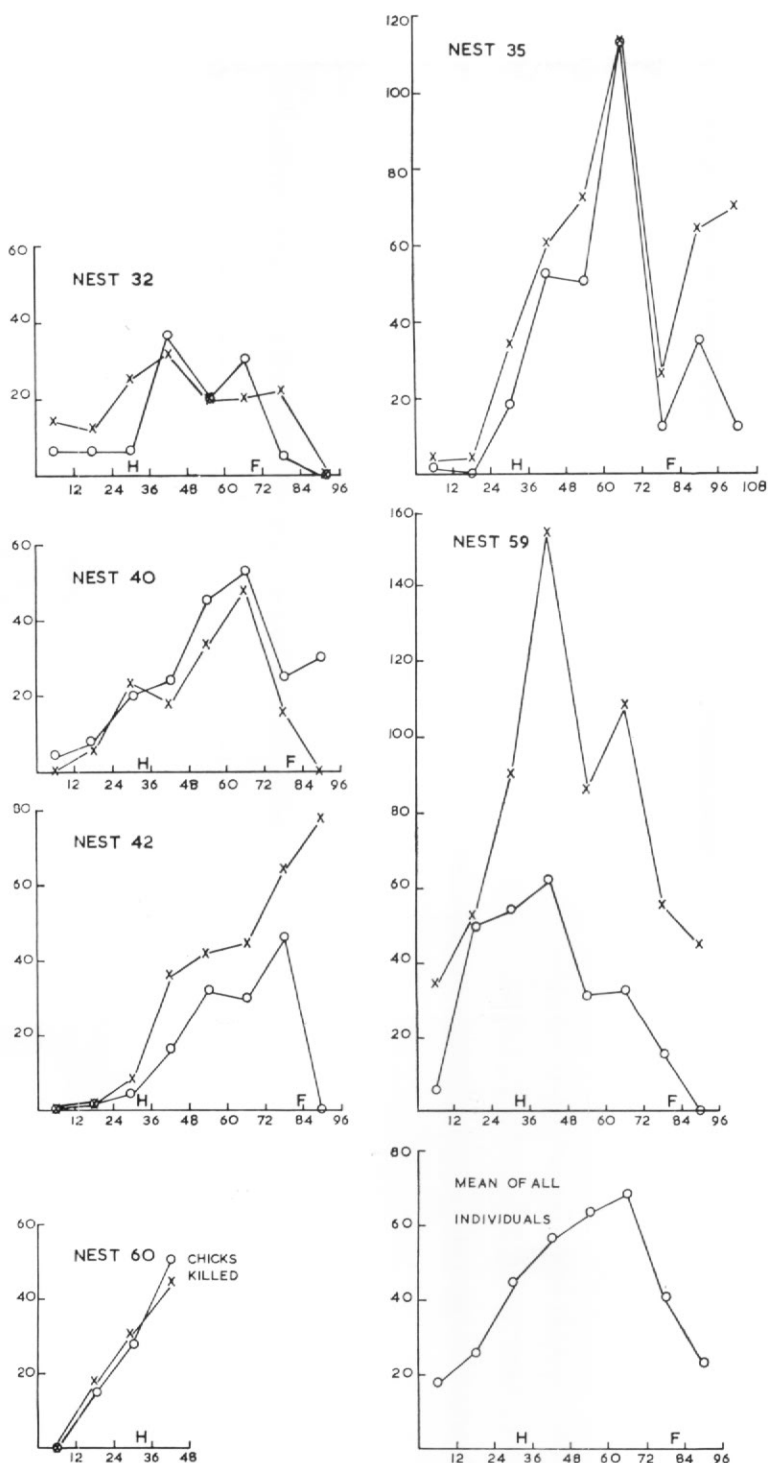


Fig. 4. Seasonal variation in response of attacks by six pairs. The ordinate is the distance (in metres) from the nest at which response is evoked, and the abscissa is the number of days after egg-laying. H. Date of hatching. F. Date of chicks flying.

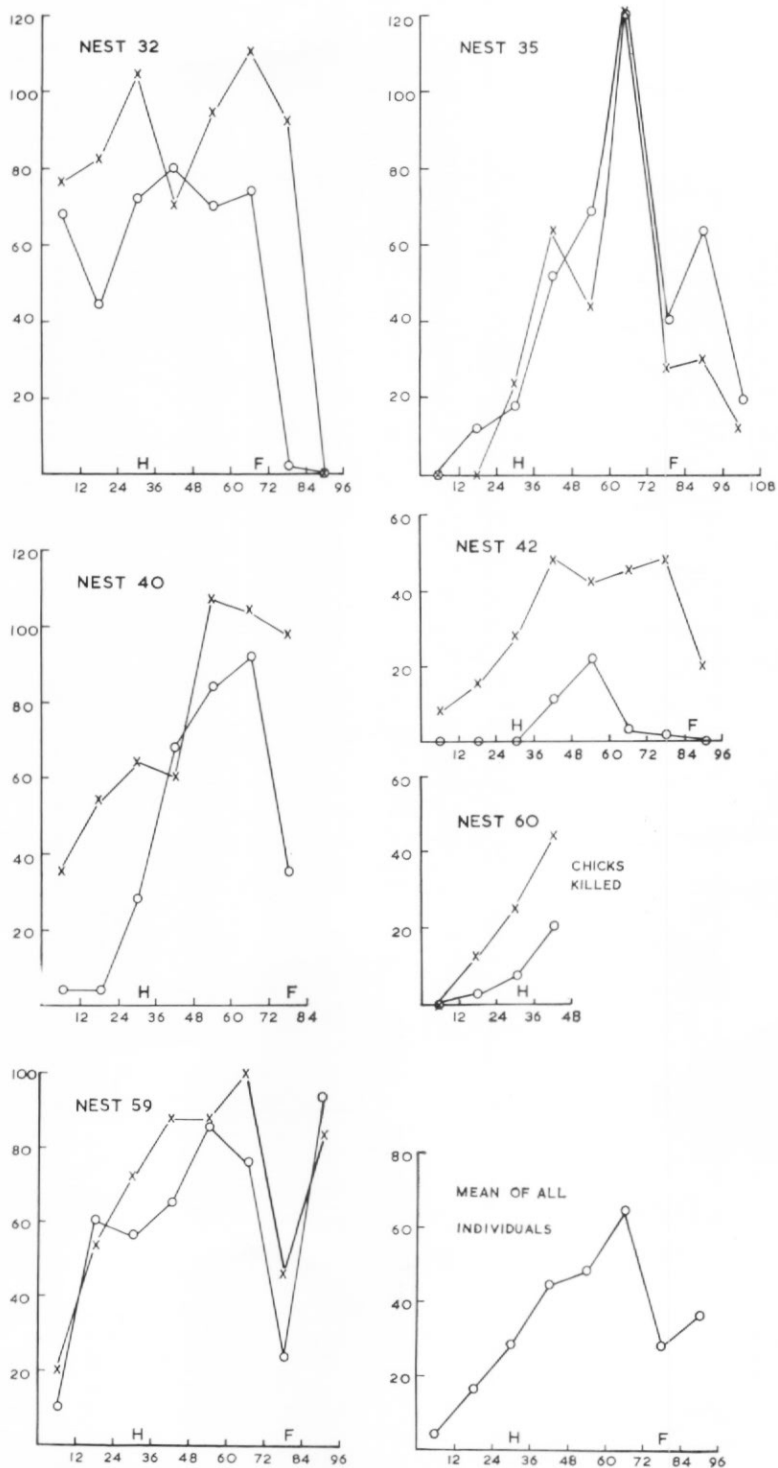


Fig. 5. Seasonal variation in response to *alarm calls* by six pairs. The ordinate is the distance (in metres) from the nest at which response is evoked, and the abscissa is the number of days after egg-laying. H. Date of hatching. F. Date of chicks flying.

Evolutionary aspects. The *swoop* and *soar* pattern of behaviour is to be found in many of the Laridae and there is a series of increasing complexity, the pattern in some of them becoming part of the courtship behaviour as in Franklin's gull (*Larus pipixcan*) (Moynihan, 1958). The pattern is not used in courtship in the Stercorariinae but the hostile aspects have been greatly developed so that skuas are regarded as very vicious birds (Perry, 1948, p. 94). Undoubtedly, the *swoop* and *soar* is the major component of the skuas' anti-predator system, although there are also passive components, such as cryptic colouring of the brood, defaecation away from the nest and egg-shell removal (Burton, 1968), which occur in other Laridae. The selective advantage of the different components of anti-predator behaviour to different predators has been shown in the black-headed gull (Tinbergen and others, 1962; Kruuk, 1964), and as components may be missing where predator pressure is relaxed, for example, the absence of egg-shell removal, etc. in the kittiwake (*Rissa tridactyla*) (Cullen, 1957), there must be similar pressures on *Catharacta*. The only recorded predators of skuas are skuas themselves (e.g. Young, 1963), Man (e.g. Moynihan, 1962) and greater black-headed gulls (*Larus marinus*) (Brathay Exploration Group, 1961). A skua will kill another that is wounded and Man kills attacking skuas that cause him to lose his temper, but principally these two species prey on the brood (at Signy Island, predation on adults and brood by both species was very slight). Other likely predators are carnivorous mammals, such as the Arctic fox (*Alopex lagopus*) but over most of the range of *C. skua* there are very few ground predators. The carnivores are most likely to be predators of the brood rather than of adults, and Kruuk (1964) has shown that in the black-headed gull attack behaviour predominates against predators of the brood, but escape behaviour predominates against predators of the adult. This would explain the preponderance of attack behaviour towards potential predators in skuas. The low nest density, compared with that of most gulls, might be an adaptation to reduce predation from the ground, since Tinbergen (1953) found that where herring gulls were exposed to predation by foxes the nests were widely spaced. The predation pressure by other skuas may also be a factor in the spacing of skua nests, as this would reduce the chances of an intruder being able to get near the brood without evoking a reaction from the parents.

The reactions of skuas to humans must have originated before the former colonized the Antarctic and they must be of a very fundamental nature, because they have survived from the time that the population became isolated until the arrival of Man within the last 100 years. Early Antarctic explorers remarked on the attacks by skuas (Wilson, 1907), so the reaction to Man cannot have arisen as a result of learning. Curio (1964) has shown that the fear of certain predators is retained by the populations of Darwin's finches (Geospizidae), although individuals have not had previous experience of them. But he also showed that the finches would react to other animals or objects that they had not seen before, so there is an inborn response to strange objects. The response to predators does not vary with experience, as Curio found similar responses by both old and young birds. This is the case of skuas' reactions to Man; in the Shetland Islands, *C. skua* has been effectively protected for 80 years but it still attacks humans. Until critical experiments are carried out by presenting known and unknown objects to skuas, the only conclusion that can be drawn is that skuas have a strong innate tendency to attack animals that come near the nest. This tendency must be deeply rooted in their genetical make-up and it is the primary method of defence of the brood.

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