

ARDEA

TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE

JAARGANG 51

MAART 1963

AFLEVERING 1

THE EARLY REPRODUCTIVE BEHAVIOUR OF THE ARCTIC SKUA, STERCORARIUS PARASITICUS (L.)

by

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(32nd Publication of the Foundation Vogeltrekstation)

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INTRODUCTION AND ACKNOWLEDGEMENTS

When studying the behaviour of the Great Skua in Shetland (PERDECK 1961) we met the Arctic Skua and the wish emerged to compare the behaviour of both species. A start was made in 1958 by Miss M. LOMBAERS, who joined us in Foula. A better opportunity came when Mr. G. PARIS and his wife invited me for a trip to the Faroe Islands. We planned to make a similar study of the Arctic Skua as we had done of the Great Skua, stressing the comparative aspect.

Although we probably managed to observe all the main activities of the species before egg laying, in one season one may easily have missed some details. I compared my data with the notes of Miss LOMBAERS. The agreement was good although she mentioned a few points

not observed by me. I have included these in my descriptions, in brackets and marked with M. L.

We like to express here our gratitude to Mr. A. NÖRREVANG and Dr. F. SALOMONSEN (Copenhagen) for advices of several kinds and Mr. and Mrs. B. DAVIDSEN (Mykines) for their hospitality. The manuscript was discussed with Dr. N. TINBERGEN and Dr. M. J. CULLEN, and I am grateful for their remarks. Dr. CULLEN kindly improved the English text.

The pictures were taken by Mr. PARIS, while his wife assisted with the observations. The drawings were made by Miss LOMBAERS, from pictures taken by Mr. PARIS.

PRELIMINARY REMARKS

The observations were made on the Faroe island Mykines from 12 May till 1 June 1961. Up to 100 pairs of Arctic Skuas were found breeding on this island. The distance between the nests, in general, was large, but a formation of colonies was apparent (Table 1). The colonies were found in swampy grounds cut up by small lochs or channels. The uneven surface seemed characteristic and its function might be to supply hiding places during the severe territorial fights. The hillocks were used as roosting places. Neither in Shetland (Noss, Foula), nor on Mykines was a typical gathering place or "club". (On Foula there was a regular gathering

TABLE 1

DISTANCES BETWEEN NESTS	
1 — 10 m : 0	71 — 80 m : 3
11 — 20 m : 0	81 — 90 m : 3
21 — 30 m : 0	91 — 100 m : 0
31 — 40 m : 7	101 — 110 m : 0
41 — 50 m : 5	111 — 120 m : 1
51 — 60 m : 4	121 — 130 m : 0
61 — 70 m : 3	131 — 140 m : 1

N.B. 24 distances were taken on Foula, Shetland (1958) and 3 on Mykines (Faroe islands).

of birds during the breeding season near a small pond, but these were primarily birds which came for bathing). Observation hides were placed in such a way that at least one pair could be watched closely, and about four other pairs were also in view. The birds of this species were much more readily disturbed than the Great Skuas. The sex of an individual could be established only after it had been seen copulating. Then

the two colour phases or, in pairs of one phase, minor colour differences could be used as individual marks. In the three pairs studied of which both birds were dark, the male was darker than the female. No difference in size, however, could be detected.

AGONISTIC BEHAVIOUR

At the beginning of our observations the territories were not yet fully established and many hostile encounters between neighbouring pairs have been watched. The territory was defended more by the male than by the female. One of the most frequent calls was the *Long Call*. It is composed of a series of loud, clearly, bisyllabic and rhythmically repeated notes ("geejoo"). The number of notes within one call varies from 1 to 12, but in most cases 3 or 4 notes are given. One note lasts about $\frac{3}{4}$ second and there is no pause between two notes. The last note from a series is often incomplete. The Long Call is heard from sitting or standing birds, as well as during flight. During the call, the neck of a standing bird is mostly somewhat stretched and at each note the head is moved slightly up and down. The bird called at is followed with one eye, frequently first one eye and then the other alternately, so that the head moves from side to side. As the Long Call is often uttered at birds passing overhead, the neck is frequently bent somewhat backwards, with the bill pointing obliquely upwards. This could be the homologue of the Oblique Posture of other species of the gull family. I am not sure of this, since they call also with a vertical neck and a horizontal bill, e.g. to birds approaching on the ground. The carpal joints are not raised (Plate I, fig. 2). Flying birds often utter the Long Call during pursuits, especially after a Swoop, when the birds soar away from each other with horizontally stretched wings.

The Long Call is often preceded by a number of short dry notes, not rhythmically repeated, which I refer to as the *Short Call*. They have the staccato character of the Alarm Call of other *Lari*, although the homology is uncertain. Most frequently they are given by birds pursuing each other in the air especially before attacking. A swooping bird calls it often just before the lowest point of its dive. It is also heard from birds standing on the ground, alternating it with the Long Call when being swooped at. When alighting after an aerial fight, a bird may go on with Short Calling for a brief time. Although this call occurs under much the same conditions as the Long Call it seems to be linked especially to real attacks in and from the air. In between the Long Call and the Short Call another call is sometimes heard, the *Yelp*. It is a high,

piercing sound, resembling the yelp of a dog. It is not rhythmically repeated, although a series may be produced. Sometimes it is bisyllabic, pointing to a relation with the Long Call. It was heard from birds being swooped at and after real chashes. It is probably the same Call which PERRY (1948) described as "yeh-yeh-wow" and he recorded it also when predators enter the colony, especially later in the season. Sometimes we heard also a harsh scream, but nothing can be said at the moment about the circumstances in which it is produced.

It was observed that the Long Call (including the posture of the bird) often drives a walking intruder away from the territory. But the Arctic Skua also possesses an *Aggressive Upright* which serves the same end (fig. 1). Just as in the Great Skua, the wings are not taken out of their pockets and the bill has no other position than in the relaxed attitude (Plate I, fig. 1). (A very aggressive male sometimes showed an *Aggressive Upright* with the bill pointing downwards. M. L.) From the latter it can be

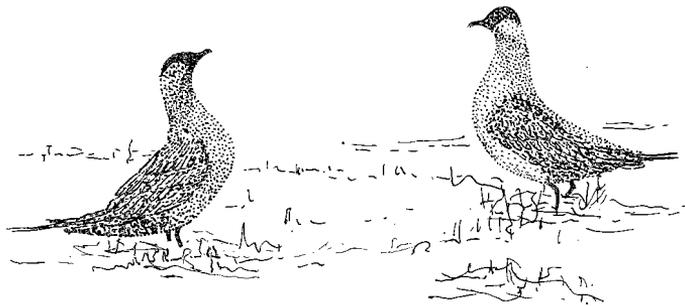


FIGURE 1. *Stercorarius parasiticus*. Right: *Aggressive Upright*.
Left: *Intimidated Upright*.

separated as a distinct posture only by the more or less stretched neck. In fact it is the same posture as the one that an alarmed bird adopts in various situations. It is also shown during the precopulatory display. Both TINBERGEN'S (1959) *Aggressive* as well as his *Anxiety Upright* might therefore be included in this *Upright*. The intimidating effect of the posture alone is very clear, although it is strengthened often by walking towards the intruder or by Long Calling. The overt agonistic behaviour following an *Aggressive Upright* is mostly an attack in the form of a peck.

In an intruding bird, threatened by the owner of the territory, the *Upright* often takes the form of the *Intimidated Upright* (fig. 1). The bill points obliquely upwards and the neck is held more or less backwards. The stretching of the neck is the same as in the *Aggressive Upright*.

A bird moving from the Aggressive into the Intimidated Upright gives a queer stiff impression, with the neck drawn back and the whole body tilted correspondingly as if it were rigidly fixed to the neck. The immobility of the posture is quite characteristic in a bird that otherwise is so very active. The owner of the territory sometimes walks round the intruder (especially during pair formation conditions). As the owner passes behind him, the intruder, standing in the Intimidated Upright, may very quickly turn his head only towards the territory holder, probably at the moment the latter would otherwise move out of sight. The immobility, and probably the posture itself too, seems to have the function of avoiding the arousal of aggression in the other bird as far as possible. The Intimidated Upright is clearly associated with a high tendency to escape, for this usually follows.

Although mild attacks on the ground are common, real fighting is done mainly by attacks from or in the air. Such fights go on for hours in succession. When the attacked bird is on the ground the attacker flies round above and repeatedly dives at him. This *Swoop* may vary in intensity. Sometimes it is mere flying at moderate height over the attacked bird. Mostly however, it is a real attack, being carried out at high speed and coming very close to the standing bird. Pictures show that the feet are lowered and one can hear sometimes that the standing bird is really hit. The behaviour of the attacked bird is of much interest. Quite often it crouches down when a swoop is to be expected, and turns to follow the swooping bird with the bill pointing towards him. At the lowest point of the swoop the crouched bird often quickly ducks its head. Between two swoops the attacked bird often runs for some shelter in a hole. Aggressive birds however, keep standing on an exposed spot, and although they also crouch, they do not duck at the critical moment. On the contrary at this very moment they jump up and attack the swooping bird from below! This remarkable counterattack I call the *Jump*. The quickness with which it is carried out makes accurate observations difficult. It was clear however that during the Jump the bird turns in the horizontal plane, thus following the swooping bird. I thought that this would prevent him from being knocked over on his back and I had the impression that the swooping bird was attacked with the bill. But Mr. PARIS has managed to make a number of photographs, showing to our great surprise, that, during the Jump, *the bird turns upside down in the air* and stakes (fig. 2) at the swooping bird with his legs, just as the swooping bird does to him. After this counterattack he turns over again and alights normally. The jumping bird sometimes staggered

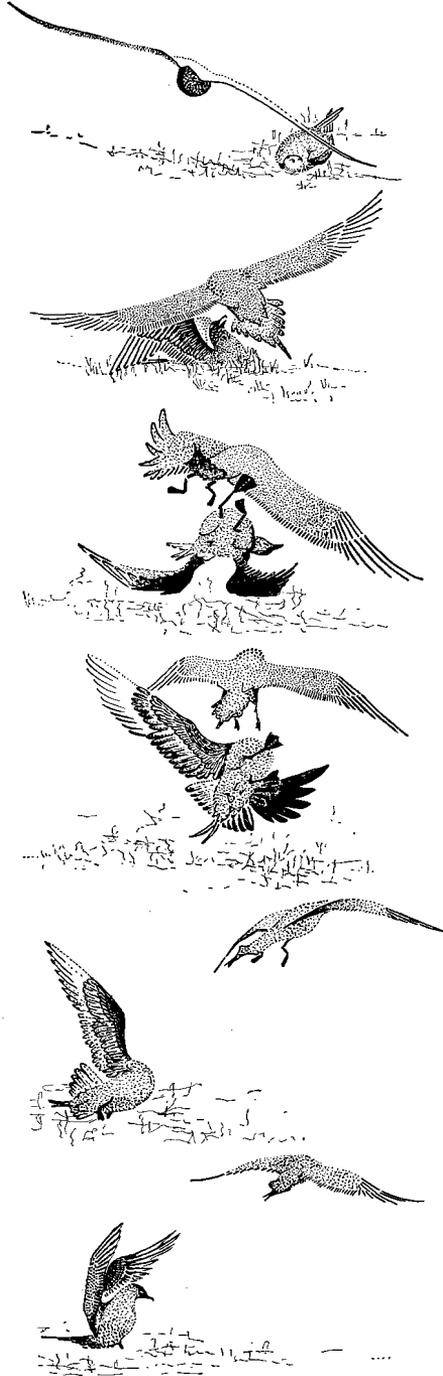


FIGURE 2. *Stercorarius parasiticus*. Swoop and Jump.

after a swoop. At first I thought that this was from being struck by the swooping bird, but now it is clear to me that this is just the end of his somersault.

After swooping for a certain time, an aggressive bird returns to alight in his own territory, and at this moment, and only rarely before, his opponent flies up and tries to swoop back at him. Apparently, the act of alighting makes a bird more vulnerable to an attack from the air since it can neither Swoop back nor Jump. (Another type of attack is when the swooping bird alights right on top of the attacked bird. This was seen in one very aggressive bird only. It also happens that, immediately after a Swoop the attacked bird flies up and follows the other bird. M.L.)

Sometimes, after aerial exchanges, the birds become involved in a ground fight. They may stand then opposite of each other and jump up with flapping wings, using mainly the legs as weapons. Beating with the wing was not observed.

More often, however, the bird that is attacked as it tries to alight, flees, and then long lasting *Pursuit Flights* may follow, carrying the birds far from their territories. The birds chase each other at top speed, pursuer and pursued probably changing roles several times. They try to strike each other and can do this from any side. If one bird swoops at the other from above, as commonly happens, the lower bird turns upside down in the air, just as in the Jump from the ground. During the Pursuits the Short Call is very common especially during chases. But, when they are ending a chase, and soar away from each other, the Long Call is given. We have already seen that the Swooping bird Short-Calls when descending, but Long Calls when ascending. An interesting observation on the calls was made when a pair was being swooped at by a neighbouring bird. Both male and female often Long Called, but in addition to this the female gave Yelps, the male Short Calls. Further, while the male fought back with Jumps, the female never did and finally hid in a hole. This observation, together with others, suggests that the Yelp indicates a stronger escape tendency, the Short Call a stronger aggressive tendency, with the Long Call as an intermediate.

Pecking into the ground as well as intensive bouts of Preening were sometimes observed in hostile situations.

MATING BEHAVIOUR

In well established pairs mating occurs often without any introductory display. The male approaches the female in the Aggressive Upright,

sometimes walking around her, while she assumes the same posture. If the female is lying down he pecks her gently at the wingtips or the back. Often, before mounting, the male makes some quick movements with the neck, which look like intention movements of pecking at the female as he does when mounted. Meanwhile the male utters a call, the *Copulation Call*. It is a high-pitched, rhythmic sound, not unlike the barking of a small dog. The female assumes the *Willing Attitude*, a posture similar to the Hunched of gulls (TINBERGEN 1959): the body is held horizontal, the neck is drawn in and the head is held at the same level as the body (Plate II, fig. 1). In most cases the carpal joints are held out a small distance from the body and the tail is not raised. When mounting, the male calls more loudly and more quickly, and keeps his balance with flapping wings. There are usually 3-5 cloacal contacts, during which the male rests with his wingtips on the ground. (Plate II, fig. 2) Especially during the contacts the female makes a soft sound (*Begging Call*). This call varies a good deal: we heard a soft purr and a not rhythmically repeated "kike". Sometimes neither male nor female call during the copulation.

Frequently the mating is introduced by a more or less elaborate display. Both birds can take a posture resembling strongly the *Begging* of the Great Skua female and I give it therefore the same name. It is mostly started by the male. He approaches the female with a lowered neck. The neck is not withdrawn but bent. This bend is accentuated often by a bulge, indicating that he will regurgitate. Then the female lowers her neck and pecks at the male's bill (Plate III, fig. 1). She may peck from below, with the bill pointing upwards or from the side, twisting her neck to do so. The male also pecks at the bill of the female and during this mutual operation the bills of both birds may be widely opened. Frequently the male makes alternating sideways movements with the neck, probably evading more violent pecks of the female. When pecking from below, the female may make short upwards movements reminiscent to the Head-Tossing of the Gulls. The female tries to peck into the mouth of the male, which he eventually opens widely while regurgitating. As a rule the female takes the food immediately from the male. The male keeps head and neck nearly horizontally while regurgitating. In both birds, the tail may be more or less raised, although I have the impression that this is more due to the slight opening of the wings (tips not crossed over tail) than to an active raising. The male, and perhaps also the female, may make a squeaking sound, similar to the sound during the nest building ceremony called Squeaking. On the other hand,

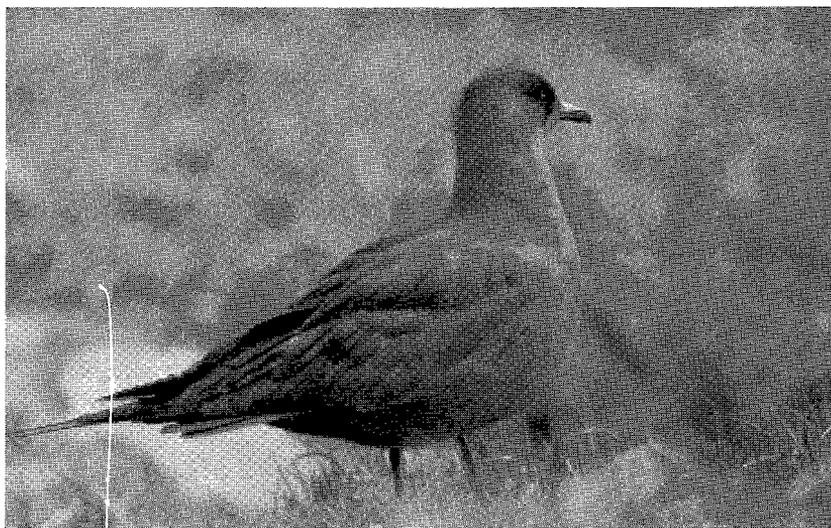


FIGURE 1. *Stercorarius parasiticus*.—Relaxed attitude.



FIGURE 2. *Stercorarius parasiticus*.—Long Call.



FIGURE 1. Female in Willing Attitude.



FIGURE 2. Copulation.

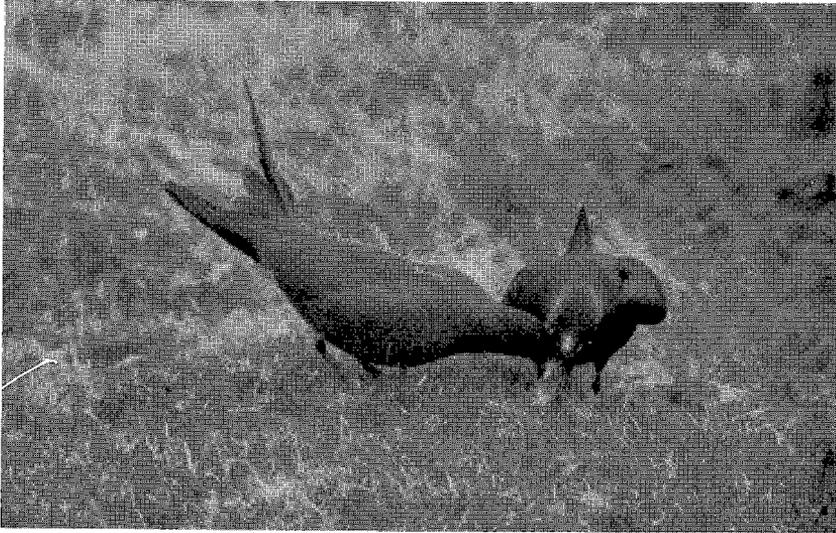
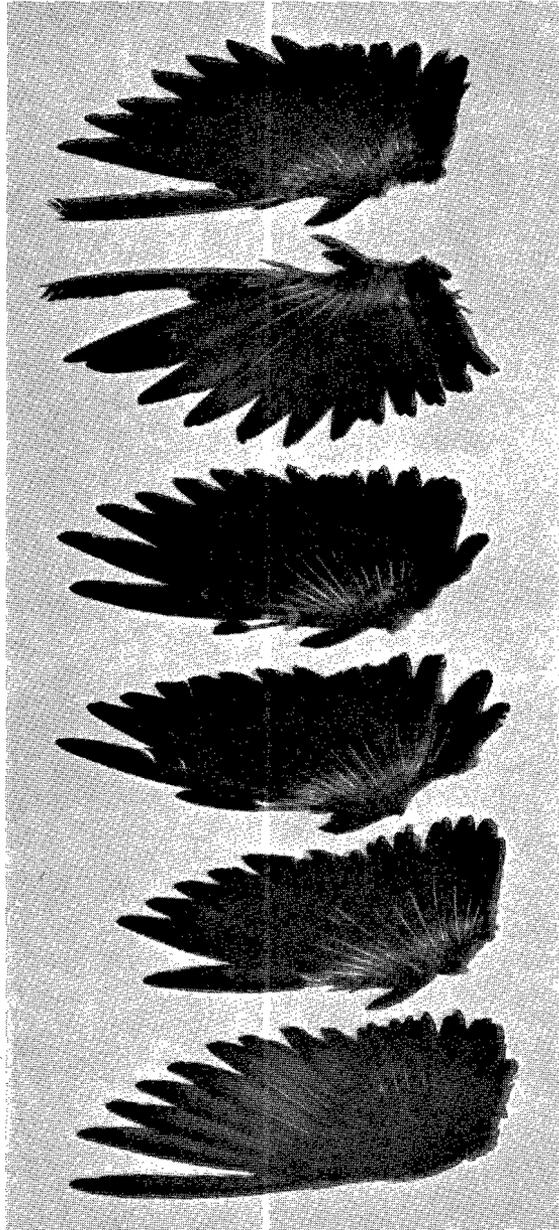


FIGURE 1. Begging.



FIGURE 2. Squeaking.



Advanced moulting stages in the wing primaries of *Hirundo rustica* wintering in the neighbourhood of Cape Town.

From top to bottom:

- 1-2. Primary 1 old, 2 moulting, rest all replaced.
3. Primary 1 just developing, rest all replaced.
- 4-5. Primary 1 in different development stages.
6. All primaries replaced and fully developed.

we also heard the Begging Call from the female and an other, not well-defined call from the male. Squeaking and Begging are in fact not easy to distinguish. This will be discussed in the next section. After Begging the copulation may follow, although in many cases the display is broken off, especially when the male has regurgitated.

The Willing Attitude of the female is quite similar to the crouched posture of a bird that is being attacked by Swoops. We noticed this clearly on one occasion. A pair was being attacked by Swoops. We noticed this clearly on one occasion. A pair was being attacked by a swooping bird. Whereas normally the birds on ground crouch only during the actual Swoop, the female kept this posture also in between the Swoops. The male then reacted with regurgitating. At that moment we realised that the posture of the female was now a typical Willing Attitude. I am inclined to believe that the crouched posture facilitated the tendency to mate in the female, as well as acting as a stimulus to the male.

NEST BUILDING

Nest building is started by one of the birds, usually the male, walking or flying from a mound towards certain parts of the territory with high vegetation. During this he makes a nasal, mostly bisyllabic sound ("hé-hé"). It is most probably homologous to the Soft Call of the Great Skua, but since it is rather loud, I prefer to name it the *Nest Call*. Often the bird starts calling already when still in the air, just before alighting. The bird may then walk around, occasionally performing nestbuilding movements, such as Sideways Nest Building, Scraping and Turning. When the female is present, she may follow the male, and, when standing together (Plate III, fig. 2), the Nest Call of both birds fuses in to the *Squeaking Call*. This Call is also mostly bisyllabic. The first part is a harsh hissing squeak, the second part lacks the squeak, but the hissing remains. The male stands usually with a slightly lowered, fairly drawn in neck, the bill pointing more or less at the ground. At times he bends towards the female with a widely opened bill (calling). The female holds her head lower than that of the male, often stretching her neck an pecking upwards or sideways to the bill of the male. He also pecks at her bill and then the postures of the birds can be quite the same. This may go on for a longer time, and meanwhile nestbuilding movements are performed, especially by the female (Scraping, Sideways Nest Building). It was observed, that, by repeating this *Squeaking Scene* the ultimate nest site was determined. In the few cases studied, it was the male that chose

the site. The real building of the nest is done mainly by the female, since she makes the most intensive nestbuilding movements. The nest is a shallow depression in the vegetation, lined with a thin layer of straws. As in the Great Skua, there is no collecting trip and all straws come into the nest by Sideways Nest Building.

We have described here Begging and Squeaking as different behaviour sequences, analogous to the situation in the Great Skua. The distinction is however, difficult to make, and apart from the Squeaking Call, the Arctic Skua does not seem to have a typical Squeaking attitude. Begging scenes are characterised by regurgitating of the male, Squeaking scenes by the nestbuilding movements. The Squeaking Call may also be heard in typical Begging scenes, although it is mainly monosyllabic then. Further, Begging is done on the mounds, Squeaking in the higher vegetation. But intermediates are very frequent and this seems to be especially the case in pairs in which male and female are not very well accustomed to each other, judging from the frequent signs of aggression and escape. In well-established pairs Begging and Squeaking are more clearly separated, and Begging is not a typical precopulatory display, but a mere feeding of the female.

PAIR FORMATION

On the first day of watching, May 12th, many pairs were already present on their territories. In the area watched five established pairs were settled. Between their territories three single birds were observed, each defending a rather small territory. As appeared later, two were males, one a female. One of the males was paired after a week and it seemed that both birds had known each other before, since we saw no "formation". The other male was visited by several other birds. On June 1st a copulation was observed with a female, that had visited him also before (May 21st). The next day, however, this female was away and another female present, with which copulation attempts were made.

The single female was one day engaged in a severe territorial fight with a neighbouring pair. She swooped continuously at them, and it could be clearly seen, that her attacks were always aimed at the female of the pair. The only result was probably a better delimitation of the territories. In the Great Skua such behaviour was seen to lead to a change of the female of a pair (on a club territory).

This single female was, near the end of our stay, visited by a male of another pair. In this pair several copulations had been observed, but the female showed regularly escape tendencies to the male (Intimidated

Uprights during precopulatory displays). His flirtations with the single female might therefore be called "redirected".

The single birds behaved in much the same manner. They stayed long on their territories and defended them against intruders, but not as fiercely as the pairs. To birds flying overhead they Long Called again less frequently than the pairs did. Occasionally, they walked through their territory, making the Nest Call and showing low intensity nest-building movements. They did not seem to have a special behaviour to attract potential mates. We could recognize two females who visited several territories in succession, not only those of the single birds, but also those of established pairs. This suggests that during pair formation the males establish a territory and that the females search for such birds. A number of meetings between these unpaired females and a single male in his territory were observed. There was no clear Meeting Ceremony as is described in the gulls. The female tried to stay in the territory, frequently flying up and returning after a short flight around. When she approached the male he assumed the Aggressive Upright and often walked around the female. She stood also in Upright, but mostly in the Intimidated Upright. Perhaps this posture serves as an appeasement gesture, comparable with the Head Flagging of the gulls in the same situation. Already in this early stage, the male tries to copulate, though this is rarely tolerated by the female. Often the male introduces a Squeaking Scene or a mixture between this and a precopulatory display, followed by nestbuilding movements.

COMPARISON WITH THE GREAT SKUA

Within the Lari it seems to be a rule that the displays are more aerial the smaller the size of the species is. Compare Gulls with Terns, large gulls with small gulls (Little Gull) and large terns (Caspian Tern) with small terns (MOYNIHAN 1959; CULLEN 1960). The smaller size seems to offer possibilities for quicker starts, accelerations and turnings in the air, all helpful to aerial displays.

This difference is also striking between the small Arctic and the much larger Great Skua. It is shown at its best if one sees an Arctic Skua attacking a Great Skua. The latter is quite helpless in the face of the quick attacks, directed from all sides, and he cannot gain enough speed to shake off his enemy. The Arctic Skua combines in a marvellous way the strength of a falcon and the grace of a tern. While I only once observed a Great Skua making Swoops at members of the same species, this is the regular territorial fighting of the Arctic. It is true that the earlier

stages of territory fixation were not observed by me in the Great Skua, but we have enough observations from both species in the time just before the laying of the eggs to be sure that this type of fighting is much more common in the smaller species. One cannot say however, that the Arctic Skua has a more ritualised aerial behaviour; it is more overt attack than display. The more aerial character of the Arctic Skua is also reflected in the poorly developed ground display. There is no clearly recognisable Oblique, no Bend and no Wing Raising. The differentiation of the calls shows the same trend. Where as, during aerial pursuits, the Great Skua only uses Long Calls, the Arctic has two other calls in addition, the Short Call and the Yelp. But the Great Skua has one more ground call, the Quick Call, mostly heard in the Intimidated Upright.

Although pair formation seems to be quite similar in both species, this seems, in the Great Skua, to be concentrated in a Club, while in the Arctic it is more spread through the colony. The club area of the Great Skua is for the greater part made up of small territories. The establishment of such territories might be difficult in the Arctic Skua since the agonistic behaviour involves so much flying. This could be one reason that the club is lacking in this species. In line with this is that, in general, the territories of the Arctic Skua are larger than those of the Great Skua.

There are some important differences in the non-agonistic behaviour of both species. Squeaking is less well differentiated in the Arctic Skua and it is often replaced by or mixed up with Begging. This Begging is a posture that the male Arctic Skua adopts also, while in the Great Skua it is limited to the female. The male Arctic Skua often takes the initiative to precopulatory or pair formation display and commonly regurgitates spontaneously, both in contrast to the Great Skua. An interpretation of these differences cannot be given. Equally difficult to understand is the presence of injury-feigning in the Arctic and the complete absence of this behaviour in the Great Skua. We have not watched it systematically and have therefore omitted a description (compare WILLIAMSON 1949).

A PRELIMINARY COMPARISON BETWEEN SKUAS AND GULLS

At the moment descriptions of the displays of two of the four living species of skuas are available. This gives an opportunity to compare them as a group with the gulls.

There are many common traits, such as the differentiation of the calls, the Upright postures, the Swoop, and Regurgitating in the precopulatory or pair-formation displays. But on the other hand some very typical postures of the gulls are lacking in the skuas, viz. Choking, Head Tossing

and Facing Away. Choking is probably represented by the Squeaking of the skuas, which shows the tilted-forward body position and is mainly distinguished from Choking by the absence of the rhythmic jerking up-and-down movements of the head. TINBERGEN (1959) points out that the absence of these movements is correlated with the absence of carrying nest material to and depositing it in the nest, using this as evidence that the rhythmic movements are derived from depositing.

Head Tossing, a common element in the sexual display of gulls, does not occur regularly in the skuas (though an action a little reminiscent of it is occasionally noticed by the female as she pecks for food from a regurgitating male). Prior to being mounted the female skua pecks for food, and only assumes the Hunched Posture on being mounted. Female gulls, on the other hand, though they may also peck for food before copulation, often show their willingness in the Hunched Posture with Head Tossing.

While most of the gulls studied have Facing Away, or something homologous to it, there appears to be nothing of this form in the skuas. The Facing Away of the gulls is inferred to function as appeasement and appears in characteristic situations in pair formation. In these situations the skuas show the Intimidated Upright, a posture also possessed by gulls and indeed to be seen in these same situations, but slightly different in form. The Upright of Black-headed and Herring Gulls ranges from the aggressive form, with bill pointing strongly downwards, to the intimidated form, with bill slightly above the horizontal. In the skuas there is also a range, but at the aggressive end the bill is seldom below the horizontal, while at the intimidated end it points much higher than do the two gulls mentioned, and probably even higher than in the Intimidated Upright of Hartlaub's Gull (TINBERGEN & BROEKHUYSEN 1954), approaching closer to what seems to be the extreme form of this posture, the Erect of terns. A significant difference in detail between gulls and skuas seems to be the position of the wings during the Upright postures. They are taken out of their supporting feathers in the gulls, but not in the skuas. TINBERGEN (1959) has pointed out that, this might be due to the fact that skuas do not fight with their wings as the gulls, substantiating the assumption that the lifting of the carpal joints in gulls is a preparation to a wing-beat. On the other hand, skuas seem to fight more with their legs and bills, both being sharper weapons than those of the gulls.

The skuas are thus seen to lack certain displays of the gulls wholly, or have them in a reduced form. This seems to be in line with the opinion

that, of the *Lari*, the skuas are the most primitive representatives. But if the ancestors of gulls and skuas were shore birds, feeding on foot along the shore line (MOYNIHAN 1959), then the feeding habits of the skuas are rather specialized, acquired later in the evolution. Morphologically they are adapted to it by the bird-of-prey-like bills and claws. Of interest is further that they have not evolved a mainly white plumage as the gulls have, confirming the supposition that the white color is an adaptation to fishing habits (see TINBERGEN 1953: 14).

One might ask in what way the feeding behaviour has influenced other behaviour. Now the method with which other birds are robbed of their food seems scarcely different from the pursuits with Swoops used against members of their own species, and the aggressive character of these is certain. If this tendency to pursue other birds to rob them of food is also aroused by conspecifics which are not too different from the species parasitised, one might expect a greater aggressiveness of the skuas compared with the gulls. Without discussing what is really meant by "greater aggressiveness" I think that skuas spend more time on overt aggressive behaviour than gulls, and that their comparatively very large territories are a result of this.

The resting on the wing tips during insemination might serve as a good diagnostic ethological character of the group. It is probably related to a different male-female size ratio (male not bigger than female as in the gulls) as I pointed out in my paper on the Great Skua (PERDECK 1960). Here also a tentative explanation of this difference between skuas and gulls was given.

SUMMARY

A description is given of the reproductive behaviour of the Arctic Skua up to the laying of the eggs. The agonistic behaviour includes two Upright postures, a Long Call and two other calls. Territorial fighting consists of Swoops and a peculiar counterattack to these, the Jump, in which the bird throws itself upside down in the air, kicking up at the swooping bird. Both Swoops and Jumps are carried out also during long Pursuit Flights. During pair formation and precopulatory display regurgitating is common. The introduction to this, the Begging is done by both male and female. Unlike the Great Skua Squeaking is not clearly different from Begging. Pair formation seems to occur on territories lying between the incubation territories.

The behaviour is compared with that of the Great Skua and the relation of some differences with the more aerial habits of the Arctic Skua is discussed. A preliminary comparison is made of the displays of skuas and gulls as groups. Attention is drawn to the poorer repertory of displays in the skuas and to the greater aggressiveness thought to be due to the parasitic feeding habits.

SAMENVATTING

In dit artikel wordt het voortplantingsgedrag van de Kleine Jager beschreven tot aan het leggen van de eieren. Er zijn twee Rechtop dreighoudingen een Long Call en twee andere geluiden tijdens het vechten en vluchten. De verdediging van het territorium geschiedt vooral door Duiken en een speciale aanval hiertegen, de Opsprong. Met deze Opsprong gooit de vogel zich ruggelings in de lucht en valt de duikende vogel aan met de poten. Duik en Opsprong treden ook op tijdens de langdurige Achtervolgingsvluchten. Voedsel opbraken door het mannetje komt veel voor bij het paringsgedrag en de paarvorming. De inleiding hiertoe, het Bedelen, wordt door mannetje en wijfje gedaan. In tegenstelling met de Grote Jager is het Piepen niet duidelijk verschillend van het Bedelen. De paarvorming geschiedt vermoedelijk op territoria tussen de broedterritoria in.

Het gedrag wordt vergeleken met dat van de Grote Jager en het verband van een aantal verschillen met de grotere activiteit in de lucht van de Kleine Jager wordt besproken. Een voorlopige vergelijking wordt gegeven tussen de „displays” van de Jagers en de Meeuwen als groepen. Er wordt gewezen op het minder rijke repertoire van houdingen in de Jagers en op de grotere agressiviteit van de Jagers, misschien veroorzaakt door hun wijze van voedsel-zoeken.

LITERATUUR

- CULLEN, M. J. 1960. The aerial display of the Arctic Tern and other species. *Ardea* 48: 1-37.
- MOYNIHAN, M. 1959. A revision of the family *Laridae* (*Aves*). *Amer. Mus. Novit.* 1928: 1-42.
- PERDECK, A. C. 1960. Observations on the reproductive behaviour of the Great Skua or Bonxie, *Stercorarius skua skua* (Brünn.) in Shetland. *Ardea* 48: 111-136.
- PERRY, R. 1948. *Shetland Sanctuary*. London.
- TINBERGEN, N. 1953. *The Herring Gulls World*. London.
- TINBERGEN, N. 1959. Comparative studies of the behaviour of Gulls (*Laridae*): A progress report. *Behaviour* 15: 1-70.
- TINBERGEN, N., & G. J. BROEKHUYSEN. 1954. On the threat and courtship behaviour of the Hartlaub's Gull (*Hydrocolopus novae-hollandiae hartlaubi* Bruch.). *Ostrich* 25: 50-61.
- WILLIAMSON, K. 1949. The distraction behaviour of the Arctic Skua. *Ibis* 91: 307-313.