OBSERVATIONS ON THE REPRODUCTIVE
BEHAVIOUR OF THE GREAT SKUA OR BONXIE,
STERCORARIUS SKUA SKUA (BRÜNN.), IN SHETLAND

by

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31st Publication of the Foundation Vogeltrekstation

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Summary
Samenvatting

I. INTRODUCTION AND ACKNOWLEDGEMENTS

The aim of this study is to give a contribution to the comparative
ethology of Lari. Although we possess at the moment more or less
complete descriptions of the behaviour of several gulls and terns,
information of Skua behaviour is only fragmentary.

When Mr. G. PARIS (Gouda) unfolded his plans to make a film of the
Great Skua, Stercorarius skua skua (Brünnich) in the Shetland Islands,
and asked me to supplement this film with notes on the behaviour,
I gladly accepted his kind invitation. I owe to him financial aid, without
which the expeditions would not have been possible.

We want to express our gratitude here for the permission of the
Nature Conservancy to work on the bird sanctuary of Noss, and to
Mr. L. A. HOLBOURN to visit his island Foula. We are indebted to Mr.
and Mrs. L. SUTHERLAND (Bressay) and Miss WISEMAN (Foula) for many

Ardea, 48
helps and lodging facilities. Mrs. PARIS and my wife patiently noted down the observations, and anyone who knows the Shetland climate can imagine that it was not such an easy job to sit for hours in the limited space of the hide.

Dr. N. Tinbergen read the manuscript and I owe to him many improvements both in wording and contents.

Dr. J. J. A. Van Iersel kindly discussed the matter at various stages, and thus helped me to acquire a better insight in several problems.

The photographs in this paper are all taken by Mr. Paris and the drawings were kindly made by Mr. M. J. C. Kolvoort, after pictures of the film taken by Mr. Paris.

II. Preliminary Remarks

The observations were carried out on the Isle of Noss from 31 May till 26 June 1957 and on the Isle of Foula from 13 May till 6 June 1958. On both islands the colonies were mainly situated on the hills, both on the tops and the slopes, some of which were fairly steep. The lower parts were less frequented. The number of pairs on Noss was aprx. 200, on Foula at least 1000.

| TABLE 1 |
| Distances between nests (Noss 1957) |
| 1 - 10 m : 2 |
| 11 - 20 m : 6 |
| 21 - 30 m : 15 |
| 31 - 40 m : 12 |
| 41 - 50 m : 10 |
| 51 - 60 m : 6 |
| 61 - 70 m : 1 |
| 71 - 80 m : 1 |
| 81 - 90 m : 2 |
| 91 - 100 m : 2 |

The distances between the nests showed considerable variation, and on some places there were clear concentrations. Mostly the distance was between 20 and 50 metres (table 1), a figure agreeing very well with that given by Perry, 1948 (15-130 yards, mean 58 yards). Incidentally, Perry's figures are not real nest distances, but distances between the mounts, which are the typical roosting places in a territory, easily distinguishable by their lower and greener vegetation. In both colonies a certain part of the occupied area was frequented by numerous birds (up to some 50 individuals) during the whole period of observation.
These birds did not breed, but rested only or showed early stages of reproductive behaviour. Tinbergen (1953) has called similar gathering places in the Herring Gull "clubs" and the same term will be used here. At Noss there was only one club, at about the same place where it was found by Perry (1948). But on Foula, several were detected. It appeared, however, that a distinction must be made between gathering places along fresh water ponds and real clubs. In the former the birds show primarily bathing behaviour and the individuals have in general no attachment to a special part of the shore when preening after bathing. In a real club, many birds hold a kind of territory (named "club territory" as distinct from "incubation territory") and reproductive activities are very frequent. The gathering places on Foula comprised two typical bathing places (Mills Loch and Overfandel Loch), one real club (on the saddle between the Sneug and the Kame) and one gathering place intermediate in this respect along a pond (Fleck Lochs).

Most time was spent in watching the birds on these clubs, since here they displayed throughout the season. The observations were made from a hide. The Bonxies were very easy to watch; it was not even necessary to be taken to the hide by another person. Identification of individuals was facilitated by the great variation in general colour (from very light brown to nearly black), and particularly in types and patterns of white patches on the head. Age classes could not be distinguished. Sexual dimorphism was nearly absent. In general, however, the males were darker and less rufous, and within a pair there is often a slight difference in size, the male being smaller. Behaviour was used as the only really reliable criterion, and particularly the Begging of the female and the Copulation Call of the male were considered decisive. The birds were active throughout the long day, and not merely in the early hours. There was, however, a typical lull of the activity in the middle of the day. The arctic character of the birds was shown by the fact that they were more hindered by warm weather than by heavy rains, storms and mist. Unlike the gulls I know, the Bonxies seldom stood long when in rest, but tended to squat.

III. HOSTILE BEHAVIOUR

In general the Bonxie gives the impression of being a very aggressive bird, in that the aggressive behaviour is quickly aroused. It is often astonishing to see how slight provocations of one bird evoke ferocious attacks in another. Frequently, intruders are not merely driven out of
the territory, but chased over long distances through the whole colony, or even further. Most of the aggressive behaviour was observed at the clubs where the small club territories are situated. Fights between owners of adjacent incubation territories were only rarely observed, but this is probably due to the fact that in both years our observations started when most pairs had fixed their incubation territories already. In the following descriptions I have adopted Tinbergen's (1959) terminology for those postures that can be considered homologous to the postures of gulls. For postures not mentioned in Tinbergen (1959) I have followed Tinbergen (1953) and Moynihan (1955).

Description

Long Call.

Just as the gulls, the Bonxies have a loud call, that is heard in a great number of situations. It is mostly given when the bird assumes certain typical postures (see below), but a bird in a relaxed, normal attitude may call also. It consists of a number of short notes, rhythmically repeated. Each note is slightly bisyllabic and has a somewhat nasal sound, although it is quite loud. One call mostly consists of 4-20 notes with a frequency of 2-3 notes per second. There are, however, variations in both number and frequency that seem to be related to different situations.

Aggressive Upright Posture (Fig. 1; Plate I, fig. 2).

To the casual observer this posture looks like the normal relaxed attitude of a standing bird (Plate I, fig. 1). The only difference is that the neck is more erect, although it remains rather thick. The bill is held in the horizontal plane, or is pointing slightly downwards. The wings are not taken out of their supporting feathers. The bird rarely calls in this posture. It is assumed by birds walking up to a Bonxie intruding into their territory and is then frequently followed by an attack. Moreover, it is a normal introduction to courtship, when both partners are standing in this position next to each other (see p. 124). It has a clear threat function, for other birds frequently move away when a bird in Upright approaches or passes them.

Intimidated Upright Posture and Quick Call (Fig. 2).

The above described posture often merges into another similar one, the Intimidated Upright, differing by an upwards pointing head and bill, and a slightly thinner neck which is often held more backwards.
Typically, it is accompanied by a variant of the Long Call (the Quick Call), in which the tempo of the successive notes is considerably quicker. If two birds meet each other in the Aggressive Upright the less aggressive one assumes this posture before fleeing. Also in the introduction to courtship aggressive movements in one of the pair often induces an Intimidated Upright in the other.

Oblique Posture (Plate II).

Like the gulls, the Bonxie possesses a posture that is especially linked up with the Long Call. The neck is rather thick, with raised hackles, and held upward or horizontal and forward. The head is in one line with the neck or more horizontal. This posture is always accompanied by the Long Call and therefore the widely opened bill is a further characteristic. The grey inside of the mouth is then revealed, but I did not find it very conspicuous is the field, though it is so in the film. The Oblique is assumed in many hostile situations and most often combined with raised wings (see below).

The Bend (Plate IV, fig. 1).

Very often, as a reaction to approaching or overflying birds, a sitting bird reacts with bending its neck, so that its bill is pointing downwards. Standing birds often assume this same posture and then the bend in the neck is still more clear. In extreme cases the bill is not pointing vertically down, but is held further backwards, reaching the breast. Often, the Long Call is given at the same time but the frequency of the notes seems lower than in the Oblique. This posture too is often combined with raised wings and also with a raised tail. Attacking birds frequently assume the Bend, often alternating attempts to attack with Bends. The behaviour gives an impression of “ostrich-policy”, but on close inspection the bending bird can be seen to follow the movements of the other bird with one eye.
Wing Raising (Plates II, III, IV).

This is the most conspicuous and typical display of the Bonxie. Both wings are stretched upwards. The angle between them varies from 45° till 0°, in the latter case the carpal joints touch each other. The white patches on the primaries become very conspicuous, and it would seem probable that these act as a signal. Wing Raising is nearly always combined with the Oblique or the Bend and is therefore not considered as a separate posture. In the Oblique the body is held more upright and so the wings are pointing upward and backward, while with the Bend the wings are held more vertically. The wings are never raised before the Bend or the Oblique are assumed. The Long Call is always given, but usually the wings are not raised until a few notes of the Long Call have been produced. During Wing Raising the birds nearly always stand. It is a very contagious posture and this often leads to a beautiful simultaneous mass display. Mostly, the birds seem to orient themselves with their body axes parallel and thus the white patches are best displayed to each other. I am, however, not quite sure whether this might not be due to the prevailing strong winds.

Bonxies often threaten each other in flight and then assume also the Wing Raising. They hold their wings stiff and stretched with an angle of about 90° between them, rather like a soaring harrier. The Bend is usually adopted then and the birds may keep this position for some time when they alight, with the wings held more upwards.

The Long Call complex.

Oblique and Bend (with or without Wing Raising) often follow each other in one smooth movement. Such sequences remind one the movements made by the Herring Gull and the Common Gull when Long Calling. But, while in these species the sequence of the movements is always the same, in the Bonxie it may vary. A standing bird may first assume the Oblique-cum-Long Call, and when still calling, raise its wings. The movement may then develop into a Bend. Or the Bend may come first, for instance in a sitting bird. He than stands up, raises the wings and stretches its neck in the Oblique. Sometimes the Oblique is followed by a Second Bend. Such sequences are rarely carried out without Wing Raising. If we denote the elements of the Long Call complex by letters (L = Long Call, O = Oblique, B = Bend, W = Wing Raising) and the sequence of Bend and Oblique by figures (1 = first and 2 = second), then the following combinations are observed: L, OL, BL, OLW, BLW, O₁B₂L, B₁O₂L, O₁B₂L, B₁O₂L, B₁O₂B₃LW.
Such combinations are very common, not only in more hostile situations, but e.g. also when a bird alights near its mate on the territory.

Raising of the tail.

Often, in combination with one of the postures mentioned above, the tail is raised to some extent. Spreading of the tail feathers was occasionally seen, but I cannot say whether this is a regular feature. Further, tail-raising can be observed only if the wing tips are not crossed and this makes it difficult to get a clear picture of the conditions under which it occurs. I have the impression that a slightly raised tail belongs to the normal posture of a bird, the tail supporting the closed wings. As soon as the wings are held more sideways the tail becomes visible and is more or less raised. A raised tail is most often seen in sitting birds that assume the Bend. Such birds often had been sleeping before, and the wings are held more away from the body, probably resting on the ground (especially when the bill is tucked inside one wing). Each time the bird bends its neck, the tail comes up; on this occasion it is probably raised actively. Definite raising of the tail was also observed during Uprights (Aggressive and Intimidated) and in the Oblique. Finally it is common in the precopulatory display (Plate V). But tail-raising seems not very strongly developed in the species, although I admit that this impression may be due to the inconspicuousness of the short tail. My observations on tail-raising were neither accurate nor numerous enough to include this behaviour in the discussion below.

Attacking, fleeing and fights.

Bonxies rarely attack each other from the air the way they swoop at human intruders. I saw it only once in a bird, presumably unpaired, but which was nevertheless holding a territory between several breeding territories. It swooped several times at a bird in a neighbouring territory, which did not attempt to fight back but merely crouched. The swooping bird was wholly silent. This kind of behaviour is perhaps more common before the territories have been established. In fact Stonehouse (1956) reports Brown Skuas frequently swooping at each other in boundary disputes in the very beginning of the season. Aerial fights are frequent, especially when the colony is disturbed, which makes the birds trespass. It is accompanied by aerial Wing Raising and Long Calling. The birds may follow each other over long distances, often twisting and turning very quickly in attempts to attack or to avoid their opponents. Real fights, however, occur only on the ground. The birds attack by moving
towards their opponent with closed or half-raised wings and wide open bill. When neither bird flees, they end up facing each other and pecking vigorously. The pecks seemed to be aimed mainly at the upper breast. They flap with the wings, but these are not used as weapons. Often a bird flies up in an attempt to attack from above (plate IV, fig. 2). Such attacks are warded off by the standing bird by lifting the body more and more backwards, the bill directed at the opponent and occasionally jumping at him. Eventually, he falls backwards. Then the birds become entangled and fight on the ground, tumbling over each other until one is lying on his back with extended wings. The other stands on top of him, holding him in his grip with bill and legs. At the moment the observer expects a murderous knockout, the victor loosens its grip and the vanquished bird flees. Such a fleeing bird often utters the Quick Call.

Interspecific hostile behaviour.

Part of this is easily observed when walking through a colony. The birds fly up, uttering the Long Call, and try to drive away the intruder by swooping (the Charge). Later in the season the swoops, famous for their fierceness, are often accompanied by a harsh scream. Before each swoop the bird hovers in the air, uttering a small number of short notes (Alarm Call). Sheep are driven out of the colony in another way, the birds flying around them with flapping wings.

Discussion

Functional aspects.

TINBERGEN (1959) has divided the postures of gulls occurring during the reproductive period into distance-increasing and distance-decreasing displays. The first promote the spacing-out of breeding pairs, the second serve or allow to bring the members of a pair together for mating, nesting etc.

The postures described in this chapter seem to belong mainly to the distance-increasing group. TINBERGEN points out, that, of course, some postures may have in this respect a dual function, according to the type of reacting individual, and the situation. He quotes the Oblique-cum-Long-Call as such, which apart from intimidating males, also attracts females, and is thus comparable with the song of passerines.

I do not know if this holds true for the Long-Call of the Bonxie, but it seems to me that in this species at least the Aggressive Upright has a similar dual function. The posture is shown especially by walking
birds, and quite often they cannot be considered to react to a special behaviour of another bird. Such birds may walk towards an intruder in the club territory or to several other birds in succession in the central part of the club. Although its intimidating effect is often clear, and real attacks on other birds are frequent, it often develops into a typical precopulatory display (see p. 124). The function of the Aggressive Upright could therefore perhaps be described as a method of finding out whether another bird is an eventual sex partner or an opponent.

My observations are not sufficient to answer the question if special functions could also be ascribed to the other threat postures (compare discussion in Tinbergen 1959).

Causal aspects.

Analysis of the motivation of displays in many species has led to the idea that they are caused often by two or more tendencies. I refer to Tinbergen (1959) for a discussion both of the methods of research and results obtained in behaviour studies of gulls.

As far as the threat postures of the Bonxie are concerned, I think that, just as in other species, the main underlying tendencies are those to attack and to escape. The overt behaviour patterns shown in quick succession with the postures are predominantly fighting, attacking and fleeing. This even holds for the Upright postures when they are shown in precopulatory behaviour, for they often alternate with mild attacks and with retreats. It must be said, however, that, except in the Intimidated Upright, where the position of the neck and head is the same as in a bird withdrawing from an attack, the postures do not contain the actual elements of attack or escape. A further question to be answered is how the relation between these two tendencies is in the different postures. In order to get an idea about this, I focussed my attention on attacking and fleeing birds, noting down the threat postures assumed just before. The result is given in table 2. Although the figures are

<table>
<thead>
<tr>
<th>Table 2</th>
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<tbody>
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<td>Threat postures assumed before attack and escape</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Before attack</th>
<th>Before escape</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>With Wing Raising</td>
</tr>
<tr>
<td>Aggr. Upright</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Bend</td>
<td>25</td>
<td>7</td>
</tr>
<tr>
<td>Oblique</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Intim. Upright</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bend-Oblique</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
small, it is obvious that in both the Aggressive Upright and the Bend the aggressive tendency is dominant, that in the Anxiety Upright the escape tendency predominates, while the Oblique is in this respect intermediate. We have no sufficient data about the quick Bend-Oblique sequences. But it seems only logical to assume that they hold a position intermediate between Bend and Oblique as separate postures.

Tentatively, therefore, a trend of increasing relative aggressiveness may be suggested in the order: Anxiety Upright, Oblique, Bend-Oblique sequences, Bend = Aggressive Upright. Nothing can be said at the moment of Wing Raising, but it may be mentioned here that it was most frequently seen in Bend-Oblique sequences, and that it was less often combined with pure Bends than with pure Obliques.

It would be of importance if anything could be said about the absolute

| Table 3 |
| Frequency of threat postures in relation to territory and strength of stimulus |
| (B = Bend, O = Oblique, W = Wing Raising) |

<table>
<thead>
<tr>
<th>For description of stimuli see text</th>
<th>Non-territorial birds</th>
<th>Birds in club territory</th>
<th>Birds in incub. territory</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Weak stimulus</td>
<td>Medium stimulus</td>
<td>Strong stimulus</td>
</tr>
<tr>
<td>B</td>
<td>6</td>
<td>10</td>
<td>17</td>
</tr>
<tr>
<td>BW</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>BO</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>BO(B)W</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>OB</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>OBW</td>
<td>1</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>O</td>
<td>10</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>OW</td>
<td>11</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Long Call only</td>
<td>3</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Total (L. Call only excl.)</td>
<td>34</td>
<td>49</td>
<td>48</td>
</tr>
<tr>
<td>% B (B + BW)</td>
<td>23</td>
<td>20</td>
<td>42</td>
</tr>
<tr>
<td>% BO (BO + BOW)</td>
<td>9</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>% OB (OB + OBW)</td>
<td>6</td>
<td>23</td>
<td>27</td>
</tr>
<tr>
<td>% O (O + OW)</td>
<td>62</td>
<td>49</td>
<td>29</td>
</tr>
<tr>
<td>% W (BW, BOW, OBW, OW)</td>
<td>50</td>
<td>45</td>
<td>6</td>
</tr>
<tr>
<td>100 B / O + B</td>
<td>28</td>
<td>29</td>
<td>59</td>
</tr>
</tbody>
</table>
level of escape and aggressive tendencies in the various postures. The structure of the club enables one to make observations concerned with this problem. In a club of Bonxies two categories of birds can be distinguished. At certain spots, mostly in the centre, a number of birds are clustered together. They pay little attention to each other and rarely react to passing birds. Near the periphery of the club, however, there are more or less fixed territories of birds that are either still in some stage of pair formation or not yet fully mature (club territories). These birds defend their territories and react readily by threat postures to intruders or overflying birds.

A limited number of counts indicate that to such a stimulus as an overflying bird the territorial birds react in half of the cases, the non-territorial birds in only one out of twenty cases. The absolute level of the tendency to react with threat postures is therefore considerably higher in the territorial birds.

We have recorded the threat postures assumed by both territorial and non-territorial birds each time we noticed other birds approaching, threatening or flying over. These situations are divided into 3 categories: 1. birds flying overhead, 2. birds flying up or alighting, 3. birds approaching and threatening (on the ground). My assumption is that category 3 represents a stronger stimulus than 2, and 2 a stronger stimulus than 1. The results are given in table 3. One may wonder why there are no Upright postures in this table. This was partly since my attention was focussed on the Long Call complex, and therefore I may have missed the Uprights, which are less conspicuous. But, on the other hand, I feel justified to say that they were very rare indeed and certainly never occurred as a reaction to stimuli of the categories 1 and 2. In spite of this gap the results are quite clear. For both territorial and non-territorial birds holds that the Bends become more frequent as compared with the Obliques as the stimuli become stronger. Further, territorial birds respond in comparable situations more often with Bends than non-territorial birds.

Table 3 does not permit to say anything definite about the sequences of Bend and Oblique, with or without Wing Raising. For Bend and Oblique three more or less established facts are now available:

(1) Bends are relatively more aggressive than Obliques.

(2) At an absolute higher level (in the territorial birds) of the tendency to react with threat postures the birds react with relatively more Bends than at a lower level (non-territorial birds).
(3) As the stimulus becomes stronger, the birds react relatively more often with Bends.

From (1) and (2) we may conclude that the absolute level of the aggressive tendency is higher in the Bend than in the Oblique. The same could be concluded from (1) and (3), if it is assumed that the absolute level to react with threat-postures increases with an increase of the strength of the stimulus. If, moreover, we assume that this raise of the absolute level concerns both the aggressive and the escape tendency, then the conclusion is permitted that in the Bend the absolute level of the escape tendency is also higher than in the Oblique.

The reactions to flying birds were also observed in the real incubation territories (last column of table 3). Here the number of bends was relatively low, which, in connection with the above might indicate that after pair formation and after having established a definite territory the birds become relatively less aggressive (perhaps in relation with an increasing brooding drive).

Comparison with the Gulls, with notes on the origin of the threat postures.

In general the hostile behaviour of the Bonxie shows much resemblance with that of the gulls (see summary by Tinbergen 1959). Just as in most of the gulls studied, the Bonxie has the Upright postures and a number of postures associated with a Long Call. There is an aerial performance comparable with the Swoop-and-Soar. But there is no Choking and Pecking-into-the-Ground occurs only occasionally.

Related Skuas from the southern hemisphere, however, have the typical “grass-pulling” (Stonehouse 1956; Moynihan via Tinbergen in litt.).

Both in the Upright and the Long Call postures there are some remarkable differences with the gulls. The Aggressive Upright differs in two points. The bill is held horizontal instead of pointing more or less downward, and the wings are not taken out of their pockets. Tinbergen (1959) considers both elements as indicating aggressive tendencies in the gulls. The lifting of the carpal joints is assumed to be an intention movement of delivering a blow with the wing. Its absence in the Bonxie is interesting, since this type of fighting does not occur in this species, and this confirms the link between aggression and the lifting of the carpal joints (Tinbergen 1959).

In the gulls the downward pointing of the bill in the Aggressive
Upright is considered as an intention to peck down at the opponent. It seems possible that this downward pecking is less typical in the Bonxie, thus explaining the lack of the downward component in the head posture, but this has to be confirmed.

The Bend is a characteristic posture of the Bonxie. Similar postures have been described in the gulls; however, here they are not clearly separate postures, but occur in a sequence of postures during which the Long Call is given (Tinbergen 1959, fig. 4). The Bonxie performs the Bend also independently of the Long Call. Although it is seen quite regularly in a sequence with the Oblique during the Long Call, the sequence may be either Oblique to Bend and Bend to Oblique. In the gulls the bending seems always to precede the Oblique or, at any rate, the sequence is rigid. The behaviour of the Bonxie suggests that the Long Call sequences of the gulls are composed of two threat postures, the Bend and the Oblique, indicating an alternation of a more aggressive tendency (the Bend) and a tendency to escape (the Oblique). The origin of both Oblique and Anxiety Upright is more or less easy to understand. On the one hand the bird tries to stay where he is, on the other hand there is a tendency to withdraw. This results in a partial withdrawal, i.e. of the head only. The origin of the Bend is less clear. The most likely possibility seems at the moment that it is derived from nest building behaviour (displacement activity). In fact, I have occasionally observed a pecking at straws during the Bend, or immediately after it. It could also be derived from autochthonous aggressive behaviour, e.g. the pecking down at the opponent, but the lack of the downward component in the position of the bill during the Aggressive Upright makes me doubt this.

Quite unique in the Bonxie is the Wing Raising during the Long Call. It is certainly different from the partial raising of the wings, the lifting of the carpal joints, as a preparatory to attack in gulls that fight with the wings. Here the complete posture is the half folded wing. But it has much resemblance to the raising of the wings after a charge (see Tinbergen 1953, plate 12a for Herring Gull), although the wings are less stretched and held more horizontal. As regards the origin of Wing Raising, the fact that a bird about to fly up has the habit of stretching its wings in just the same manner may be significant. The body is then held horizontal and head and neck are stretched forward. The first wing beat which brings the bird from the ground is made from this position of the wings. Also, males that are trying to mount a female before copulation often hold their wings in the same way as a preparation
for the short flight onto the female. Wing Raising therefore seems to be derived from an intention movement to fly up.

IV. MATING BEHAVIOUR

Description

Matings were observed frequently in the clubs and, before egg-laying, in the established incubation territories. The first introduction is mostly the Aggressive Upright posture, assumed by both birds. When one of the birds is more aggressive, then the other bird may assume the Intimidated Upright. Next the neck becomes a little more curved in both birds, and often they walk round each other in this posture. If the female takes the initiative, she lowers her head and tries to come in front of the male, sometimes walking in small circles before or around him. The feathers of the neck are strongly ruffled so as to form a pronounced bulge (Plate IV, fig. 3). Gradually she lowers her neck further and often touches the breast and the bill of the male with her bill. The neck is not withdrawn as in the Hunched of the gulls. The tail is often raised. Occasionally she may make short upward movements with her head, reminescent to the Head-Tossing of the Herring Gull. This behaviour is called Begging. It is accompanied by a soft purring sound (Begging Call), sometimes given in a phrase of about 3-4 rhythmical notes, and sometimes quite similar to the Soft Call (see p. 130). The male may react to this by uttering short rhythmical sounds, that bear a certain resemblance to the notes of the Long Call, but they are less hoarse.

The bill is not always closed between the notes. Frequency and volume of the notes vary together. As both increase, the bird stretches its wings in a manner quite similar to the Wing Raising and the preparation to flight (p. 123). This stretching is repeated several times and gradually the bird makes one or more wingbeats, thus lifting himself from the ground and turning so that he is at right angles to the body of the female (Dancing) (plate V, fig. 1). Especially as a reaction to bouts of higher intensity of the Copulation Call the female assumes the Willing posture. She withdraws her neck (as in the Hunched of the gulls), and lift the wings out of the supporting feathers so that they stand a little away from the body. The tail is always lifted (plate V, fig. 1). Now the male mounts (mostly after some failures) and tries to copulate. In well-established pairs the female may adopt the Willing posture only when the male is mounting. The male balances by flapping his wings, and keeps on calling (plate VI, fig. 1). During each contact,
however, he is noiseless. These contacts are performed in the same way as in other gulls, the male resting on its tarsi and wagging its tail. A typical feature is, on the other hand, that the male Bonxie supports itself on its wing-tips during each contact (plate VI, fig. 2). In a few cases we were able to see the tail position of the female. It was not

<table>
<thead>
<tr>
<th>Type of behaviour</th>
<th>Number of cases</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. ♀ Beggs (51)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. ♂ Calls, Dances</td>
<td>(13)</td>
<td></td>
</tr>
<tr>
<td>2. ♂ Regurgitates</td>
<td>(18)</td>
<td></td>
</tr>
<tr>
<td>3. ♂ nesting behav.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. ♂ other behaviour</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B. ♂ Calls, Dances (25)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. ♀ Willing attitude</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. ♀ Beggs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. ♀ nesting behav.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. ♀ other behaviour</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N. B. Each sequence has its beginning in A or B. Continuations are shown by the arrows.

raised, but horizontal and more or less covered by the lowered wing of the male. The number of contacts per copulation varies from 1-9. The female may continue to utter the Begging Call and often pecks upwards at the breast of the male. The male also pecks, sometimes very
vigourously, at the female’s head, especially when she does not assume the correct posture. There is no typical afterdisplay.

This typical behaviour may be varied in many ways. Sometimes the introduction is simpler. For instance, after the Upright, the male may Call and Dance, and then the Begging of the female is often suppressed. In well-established pairs, in the incubation territories, the precopulatory display can be even shorter, the female just standing, and the male mounting without preliminaries, after which the female assumes the Willing attitude. Or there may be complications. Often, the male regurgitates as a reaction to the Begging of the female (plate IV, fig. 3). A first sign of this is that he raises its hackles, obviously pressing food into his neck. This posture may be quite similar to low intensity Begging of the female (plate V, fig. 2). Intensive Begging by the female, and aggressive tendencies on her part seemed to elicit Regurgitating most readily. If a male did not react quickly to a Begging female and tried to withdraw, she followed him and tried to come in front of him, frequently pecking at his breast. Such a begging female might pursue the male over quite a distance.

TABLE 5
Number of contacts during copulation

<table>
<thead>
<tr>
<th>Number of contacts</th>
<th>Club territories</th>
<th>Incubation territories</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

If the male regurgitates the food is always eagerly eaten by the female. Next the birds clean their bills by wiping of pecking into the wet, mossy surface, after which, as a rule, they proceed to drink. Then the male may start with Calling and Dancing, sometimes after the female has begged anew, and this leads eventually to a copulation.

In order to give an idea of the various complications that may occur, the sequences observed in 76 precopulatory displays performed at the club territories are given in table 4. A few conclusions may be drawn from this table. Nesting behaviour is common after the display has broken off. This will be discussed in the next chapter. The chance that
Fig. 1. Bonxie in relaxed attitude

Fig. 2. Aggressive Upright in precopulatory display (central bird)
Obliques with Wing Raising
Fig. 1. Bend with Wing Raising

Fig. 2. Fighting birds

Fig. 3. Begging female (left), male Regurgitating
Fig. 1. Male Calling and Dancing, female Willing Attitude

Fig. 2. Male showing intention to Regurgitate (frontal bird)
Fig. 1. Male mounting for copulation

Fig. 2. Copulation
the courtship proceeds further, and eventually leads to a copulation is smaller when the male reacts with Regurgitating than when he Calls and Dances (after 31 cases of Regurgitating 2 copulations, after 21 occurrences of Calling and Dancing 9 copulations). The female seems to be more likely to adopt the Willing attitude in response to the Dancing and Calling of the male when she had begged before than when the male had taken the initiative.

The behaviour in the incubation territories was somewhat different. The male reacted more readily by Regurgitating to the Begging of the female, and other displays, such as nesting movements, were rarer. He more often simply fed the female. When, however, the female had adopted the Willing attitude, a successful copulation inevitably followed (in the club territories this happened in only about half of the cases). A further difference was that the number of contacts in each copulation was in general higher in the incubation territories than on the clubs (table 5).

Some words must be said about what has been called “other behaviour” in table 4. If the male did not react by Calling and Dancing, Regurgitating or nesting movements to the Begging of the female, he usually flew or walked away and quite often went to the club centre and not uncommonly courted another female there. The “other behaviour” of the female in response to Calling and Dancing and real copulation attempts by the male often consisted of aggressive behaviour either against the male or against strange birds at the club centre.

Discussion

It is, of course, not yet possible to give an interpretation of the Bonxies precopulatory behaviour in terms of underlying tendencies. But it is quite apparent that, next to the sexual motivation, aggressive and escape tendencies are very common. Not only the initial Upright postures point to this, but also the pecking of both birds at each other and the frequent evading of one of the birds. Since both nest building behaviour and regurgitating are commonly interspersed in the displays, these two tendencies are also present. Our general impression is that in the club territories aggression and escape play a very important role, and that many variations depend on the relative strength of these two tendencies (e.g. each of these inhibiting the nestbuilding or the sexual tendency). In the incubation territories, on the other hand, the behaviour seems to be largely governed by the nestbuilding and the sexual tendency (these being then stronger and inhibiting each other).
The Begging of the female is probably a more aggressive attitude than the Willing Posture. And the Dancing of the male may be more aggressive than the Regurgitating. This is concluded from (1) the elements of aggression in the postures (e.g. pecking and pursuing in the Begging, pecking and flying above female in the Dancing) and (2) the overt escape and aggressive behaviour occurring before or after the posture in question. Regurgitating seems especially to be fed by escape tendencies. It is significant that gulls, followed by Skuas, and trying to escape, regurgitate regularly. Stonehouse (1956) describes how chicks of the Brown Skua really drive away their parents from food in the Begging attitude, at the same time inducing them to regurgitate.

The sexual tendency of the male and Regurgitating seem to inhibit each other. For copulations occur less frequently when the male has regurgitated, although the female shows the appropriate behaviour (table 4). When, years ago, I watched the Herring Gull, this same phenomenon was observed. Further Regurgitating rarely occurs in the precopulatory display of well-established pairs, that have a higher sexual tendency (as may be deduced from the higher number of contacts during copulation).

A few remarks may be given on the functions of the various behaviour elements. The clear signs of aggressiveness in the precopulatory display of the Bonxie raises the question if there are any special appeasement gestures, reducing the chance that a real fight develops. A special appeasement gesture, such as Head Flagging, has not been observed. For the moment I would suggest that the Anxiety Upright, a quite common posture in the first stages of the display is the functional equivalent of Head Flagging in the gulls. But it must also be mentioned that Regurgitating of the male followed by the eating of the food by the female, made the females less aggressive. Since copulations are rare after this feeding of the female the effect is, however, more a long range one, dealing with the formation of the pair, rather than serving the establishment of a copulation directly. In this sense Regurgitation seems to have a similar function as the Squeaking, a special kind of nesting behaviour (described in the next section) that frequently occurs after a precopulatory display has been broken off.

The unshortened neck and the absence of Head Tossing makes the female precopulatory display quite different from that of the gulls. Here the Hunched and Head Tossing are identical to the begging for food as shown by the halfgrown and older young, and one may ask if the young Bonxie begs differently from young gulls. I have no obser-
vations on this, but STONEHOUSE (1956) reports that in the Brown Skua, who also lacks Head Tossing, the begging of female and fledglings was similar. The skuas further differ from the gulls in that the male supports itself during the insemination with the aid of the wingtips. It has been suggested that this is related to the fact that the Bonxie is such a heavy bird, that cannot hold its balance so easily. But the much smaller and very swift Arctic Skua does the same and large gulls such as the Herring Gull and the Greater Blackback do not seem to need such a support. Perhaps this behaviour has to do with the following. Whereas in the gulls the male is bigger than the female, in the Bonxie the situation is more or less reversed. It seems to me that, when resting on its tarsi, the male Bonxie has to move so far backwards on the back of the female, that he cannot hold on to the female's shoulders and therefore needs an extra support. Finally the aggressiveness of the female must be discussed. In the gulls the male is in general more aggressive than the female and the defending of the territory is done largely by him. In the Bonxie, however, quite commonly the female defended the territory more than the male. This again may have to do with the greater average size of the female. Within a species, larger individuals seem in general more aggressive than the smaller ones. This may partly be due to the intimidating effect of size as such. I have observed a pair (in a club territory) of which the female was much larger than the male. It was interesting to see the female continuously Begging with nearly no signs of aggression, while the male reacted mostly with Regurgitating or Squeaking. Even after being fed several times, the female continued begging, indicating by the way that she “begged for a copulation” not for food. I got the strong impression that the male was scared by the large size of his mate.

Perhaps, the piratical or sometimes really preying habit of the Bonxie has to do something with the reversed male-female size ratio, as compared with the gulls. In birds of prey the same thing is found (male smaller than female) as compared with e.g. passerine birds (male larger than female). The relation is probably as follows. A predatory bird needs a high aggressiveness to other birds, that may be not only of equal size but also of the same general appearance (Bonxies predate gulls).

But this high aggressiveness is a drawback in the pair formation and the mating. Now a male has to perform the most “aggressive” part of the mating, viz. mounting the female. It has therefore survival value that the male is in general more aggressive than the female. But he must, of course, not be too aggressive. The chance that this occurs is greater in a species that, for reasons of feeding, needs an extra dosis of aggressiveness. For such a species a reduction
of the size of the male (relative to the size of the female) therefore might have survival value.

V. Nest Building and Early Breeding Behaviour

Nesting and breeding behaviour in the incubation territories

As has been said before, most time was spent in watching the birds on the club. Nesting behaviour was very frequent here, but the nests were never completed. In order to get a picture of the normal complete nesting behaviour of an established pair, and moreover to study the early breeding behaviour in general, 9 days (May 15-23, 1958) were spent near an established territory at a distance from the club. The sexes were easily recognisable since this male had much white on the head, the female not. Additional observations were done in surrounding pairs. Copulations were still frequent and most pairs had no eggs. At the beginning of the observations there was in the territory I watched no nest, but there were some scrapes. On May 17 the first egg was laid. In order to observe the nesting behaviour once more I removed this egg and filled up all scrapes. On May 22 the next egg was laid.

Nesting behaviour.

The first stage in the nesting behaviour consists of the bird walking slowly through its territory, in a typical searching fashion. It often looks down, and sometimes pecks in the ground, occasionally pulls out a little straw and simply drops it again. Gradually the bird begins to favour certain parts of its territory, and when walking utters a simple soft call, consisting of one note (Soft Call). The posture of the bird is slightly different from the normal attitude, the head is somewhat lowered and the neck slightly drawn in. This posture becomes more distinct as the bird approaches a nesting site (Nest Approach attitude). On favourable sites, such as natural depressions in the ground, the bird lowers its breast, keeping head and neck in the normal attitude, makes alternating scraping movements with the legs and sits down (Scraping). During scraping the carpal joints are held a little away from the body and the Soft Call is often uttered. Between bouts of scraping, the bird stands in the scrape, pecks in it, and turns over a varying angle (Turning). In this way, a number of scrapes are made in the territory. The highest intensity of nest building seems to be what is called in other Lari “Sideways Nest-Building”. The bird picks up a straw, or pulls it out, and throws it backward with a sideways movement of the head. During this
movement the bird may sit down or stand in the nestsite, or a little away from it. The whole layer of straws, which is sometimes quite thick, is formed by this movement. Collecting of nestmaterial away from the nest, carrying it to and depositing it in the nest never occurs. This was safely established by removing the whole layer of straws from nests with eggs. After a day there was again a considerable amount of material in the nests, whereas the observations of the birds never revealed any collecting, but only sideways building.

Selection of nest site. Squeaking Ceremony.

Whereas all the behaviour described until now may be performed by either male or female when it is alone on its territory, other behaviour, clearly related to nest building, is seen when both birds are present. One of the birds walks towards a certain scrape, uttering the Soft Call and gradually assuming the Nest Approach attitude. Then it is followed by the other bird. When both birds are together the Soft Call is replaced (through intermediates) by very high squeaking notes, that are produced with the bill wide open. Mostly both birds call together. During this call the bird assumes an attitude quite similar to the Nest Approach attitude, but with the difference that the body is more tilted downward. This posture, together with the call, will be referred to as Squeaking (plate VII). Either one of the birds may stand in the hollow and perform Scraping, Turning or (less regularly) Sideways Building, or both hold their heads above the nest site, occasionally pecking at each other's bill. In the pair studied a clear difference between male and female was observed. The male attracted the female more to the places where he was Squeaking and when she arrived he stepped into the nest (if he was not already standing in it), Turned, lay down, and stepped out of the nest again, constantly Squeaking. Often the female then stepped into the nest and Scraped. Although the male might do some Scraping when on the nest, he did so far less frequently than the female. The whole performance suggested that the male indicated the nest site to the female. In fact, from 27 Squeaking Ceremonies (i.e. when both birds are Squeaking close together) the male attracted the female in 19 cases, the female the male in 8 cases. When I removed the first egg, and filled up the nest and the other scrapes, both birds were at first still attracted to the nest site. But the male began to favour a new place, to which it attracted the female by Squeaking. The female deposited her second egg in this new nest. The observations do not, of course, permit to conclude that the male is always the one who fixes the nest site. The
function of the Squeaking, however, seems clear. It ties both birds to a few sites in their territory, of which one is finally chosen. In the surrounding territories too Squeaking was very frequent before the eggs were laid. Shortly before laying the first egg the female intensified her Scraping movements considerably and probably just before and after the laying she does a great amount of intensive Sideways Building. Breeding of both birds started now immediately.

Nest Relief.

Incubation behaviour was not watched systematically, but we have seen many nest reliefs and a short sketch can be given. The relieving bird mostly approaches in the Nest Approach attitude, often calling (Soft Call). The sitting bird may start calling too. Then the Soft Call is replaced by Squeaking and sometimes a real Squeaking Ceremony develops. Sideways Nest-Building is frequently seen in reliefs; it is done mainly by the relieved bird (in 20 reliefs this behaviour was shown by relieved bird only in 10 cases, by the reliever only on one occasion, by both birds on 3 occasions; and in 6 cases no nest building was seen at all). In one pair the male never made nest building movements when relieved, the female always. This seemed to be caused by a difference in broodiness, for the male frequently left the nest spontaneously, which the female, a much better sitter, never did. In some cases the sitting bird simply steps off the nest quietly and the reliever settles.

Nesting behaviour on the club

Although nests on the pairing territories were never completed with a layer of straws, nesting behaviour was very common. It was carried out mainly near one of the scrapes in the territory, several of which were frequented. All the movements described above occurred, and they were of the same form. They were, however, usually connected with aggressive and courtship behaviour (mostly with a combination of the two). Nesting movements were never used as a threat posture to birds of adjacent pairing territories. Sometimes, nesting was clearly connected with attacks on such birds, but then it occurred after the attack. Incomplete matings were usually followed by nesting behaviour. It was then shown either by one or by both birds. If both birds took part, it frequently took the form of the Squeaking Ceremony. The initiative to this was mostly taken by the bird that broke off the courtship. Thus, on 26 occasions on which nesting behaviour occurred after
Begging by the female (or after Regurgitating and eating), she started the nesting only 5 times. On 10 occasions when the male vainly courted the female with Calling and Dancing, the initiative to nest was his only once. In about half the cases the nesting developed into Squeaking Ceremonies. In general, the nesting movements of the male were less intensive than those of the female, and particularly Scraping was more frequent in the female.

VI. PAIR FORMATION BEHAVIOUR ON THE CLUB

Both in 1957 and 1958 most territories seemed to have been established already before our arrival. But during the whole period of observation unmated birds or not yet fully established pairs were present at the clubs (plate VIII). I am aware of the possibility that observations earlier in the season might reveal that the club behaviour described below is not that of the usual pair formation. But several stages of pair formation could be seen on the club, and although they usually did not lead to breeding, a description of these stages remains of interest. The club is not a haphazard gathering of birds. Often one is able to distinguish clearly two parts in it. In the central part the birds are close together, they fight less and react only slightly to approaching or overflying birds. There is no attachment of the individual bird to a special part of the club. This part is real “no man’s land”. It is also the most trodden place of the club. Long use by many generations of birds has given it a very special appearance. The peripheral part, where the vegetation becomes gradually higher, is mainly used by birds that show typical territorial behaviour (club territories). The individuals stick to special parts of it and are very aggressive against intruders. They also threaten more readily against overflying birds, and in general assume more aggressive threat postures (compare p. 121). Most of these birds are mated and sexual displays, including copulations, are common. The members of a pair remained rather aggressive against each other. Redirected mating attempts at other birds in the central part of the club were not infrequent, especially of males after unsuccessful copulations in the club territory.

Although they do not build real nests, several scrapes are made in each territory at which the birds perform all the typical nesting movements, Squeaking being very common. Often the first contact seems to be made in the central part of the club. Among the quietly sitting birds one individual walks in the Aggressive Upright. It often chases away other birds, but finally stops near a certain bird. If this bird is asleep
he wakes it up with a peck. If the first bird was a male and the other a female, the male begins to call his Copulation Call and tries to copulate. In general the female will not accept this so readily, she threatens (often with Bends) and pecks at the male. Eventually she reacts by either Begging the Willing Attitude, or sometimes with a mixture of these postures. The copulation attempts are not successful. If the female took the initiative she assumed (after the Upright and perhaps after pecking the other bird) the Begging attitude. This induced either copulation attempts in the male or Regurgitating (this latter especially if the female had been aggressive). Of course, these first initiations are usually incomplete, since the approached bird is not willing and short clashes ensue. Once a male approached another sleeping male, woke him up with a peck, and gave the Copulation Call. Then both birds assumed the Aggressive Upright and the approached bird regurgitated and after that attempted to copulate with the other male (with Calling and Dancing).

One often sees that a bird that has failed to establish contact with one bird, walks away and proposes to another bird. I think these meetings lead to more prolonged contacts only between birds that know each other already. After an unsuccessful copulation attempt, or regurgitating, one bird, followed by the other, walks away to the peripheral part of the club and a more or less typical Squeaking Ceremony may follow. It seems that, repetition of this behaviour by birds that stay together gradually results in the establishment of a territory in this part of the club. Even though such birds with awakening sexual motivation may still frequent the central part of the club, they are clearly more territorially minded and probably become better acquainted to each other.

Sometimes a single bird settled between the club territories. The behaviour of such birds was very peculiar. Single females kept near one special territory and persistently tried to court a male whose own female was absent. Such interlopers frequently make nesting movements, combined with the Soft Call. They often join (at a distance) the Squeaking Scene of the pair. And, unlike first meetings in the centre of the club, they try to induce their favoured bird into Squeaking.

In one case we were able to follow the whole sequence. The intruder had an increasing success with her flirtations and the male became more and more aggressive against his own mate. At the end she was, after heavy fights, driven away by the male and the intruding female together.

A single bird may hold also a territory between the other club territories. It defends it, and frequently makes nesting movements. Certain birds are not driven out of the territory but induced to join in preco-
pulatory displays (often preceded by and ending in Squeaking). Such birds were observed to have several temporary mates in succession. If pair formation takes place on the club, then pairs, once definitely formed, have to move from the club to an incubation territory. We did not actually observe this, but on a few occasions certain pairs that had held territories on the club for some time disappeared, probably to settle elsewhere. It seems likely that such new pairs have to move from the central part of the colony to the peripheral parts, where there is still unoccupied ground. In fact, we found here pairs that held a territory, but did not proceed beyond making one or more nests without laying eggs. The nests were well-built (lined with grass). Birds moving out of the club are therefore not necessarily fully mature.

Summary

The reproductive behaviour of the Great Skua was studied in Shetland during two seasons. My main aim was to provide good descriptions for a comparison with the gulls.

Territories are large and a communal gathering place, the club, is present. Hostile behaviour comprises gull-like posturing like Uprights, Oblique and Long Call, but also a Bend and Wing Raising. Choking is absent. A limited set of quantitative observations enables a few conclusions about the causation of threat behaviour.

Fighting does not include wing beating. In precopulatory display Uprights are common. The analogue of the Hunched in female gulls is different, the neck not being withdrawn. There is no Head Tossing. Regurgitating of the male is common, but in general does not lead to copulations. The female is rather aggressive during precopulatory display and it is suggested that this situation, reversed as compared with the gulls, is related to the predating habit of the species and with the greater size of the female. Nest building lacks the collecting trip and the depositing of nest material. There is a special behaviour, the Squeaking, that has a function in fixing the nest site. Pair formation could not be studied, but the behaviour on the club related to this is described.

Samenvatting

Het voortplantingsgedrag van de Grote Jager werd gedurende twee seizoenen bestudeerd op de Shetland eilanden. De opzet was een goede beschrijving te geven opdat vergelijking met de meeuwen mogelijk zou zijn.

Literature


Über die Schnappbewegung des Fischreihers,
Ardea cinerea L.

Von

G. P. Baerends und J. M. Baerends-van Rooin 1)

Zoologisches Laboratorium, Groningen, die Niederlande

Auf Seite 152 unserer Arbeit über die Ethologie von Cichliden (Baerends und Baerends-van Rooin 1950) haben wir, in einer

1) Herrn Prof. Dr. O. Koepler zum 70. Geburtstag gewidmet.