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UNITS OF BEHAVIOUR IN THE BLACK-HEADED GULL, *LARUS RIDIBUNDUS* L.

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Abstract. The present paper makes a plea for the development of methods for classifying behaviour in a systematic way, by which relevant sources of information are less likely to be neglected than in the conventional intuitive way of classifying behaviour. Film-analysis of the behaviour of the black-headed gull revealed that more details can be distinguished than was suggested by earlier descriptions. For a study on communication between individuals of this species, a new objective classification has been designed, in which special attention is paid to the position of the different parts of the body. It is based on a very large number of categories of behaviour. Most of these categories occur only a few times, and consequently the statistical treatment of the material is extremely difficult. The number of categories has therefore been reduced by joining categories which are similar with respect to form, motivation, and information content. This final classification is compared with earlier ones, and advantages are discussed, and exemplified by two postures whose unique properties were revealed by the present procedure.

Formerly, when bird-watchers were equipped with only field-glasses, pencil, note-book, and in exceptional cases with a tape-recorder, the descriptions of sequences of behaviour were simple and contained a small number of different behaviour elements. The observer had to be able to identify and record the different units of behaviour as fast as the animal performed them. This was the most important restriction on the number of categories which could be distinguished. It was assumed that the forms of many of these categories were very stereotyped ('fixed action patterns').

With the development of film and video recording techniques, the forms of some 'fixed action patterns' were subjected to a closer examination. In a number of cases, like the actions of the goldeneye duck (Dane et al. 1959; Dane & van der Kloot 1964), they did turn out to be very stereotyped. In other cases, such as the facial expressions of cats (Leyhausen 1956) and dogs (Lorenz 1963), an almost continuous variation appeared to exist. In view of this variability Barlow (1968) proposed that the term be changed to 'modal action patterns'. At the same time much more detailed descriptions of behaviour could be made than before, sometimes approximating perfection (Golani 1976). A disadvantage of these detailed descriptions was that statistical treatment of the material became extremely difficult.

When starting their study on communication in the black-headed gull, the members of the Groningen gull research group found that the existing classifications, of Manley (1960) and Moynihan (1955), were not suitable for a sufficiently detailed description of filmed encounters between the birds. Displays seemed to be much more variable than was suggested in earlier studies, and between displays many kinds of intermediate forms were possible. Since details in gull displays (and in their associated vocalizations) may have functional significance (Beer 1975), it was decided to develop a method for obtaining classifications of behaviour in a systematic way, which would reduce the chance of neglecting possibly relevant elements of information.

Detailed Description of Behaviour

All behaviour sequences referred to in this paper had been recorded on video. Each frame was supplied with a visible time-signal in tenths of seconds. By slow-motion play-back, freezing frames where necessary, the behaviour sequences could be accurately transcribed along a time-scale on pre-printed lists. Each sequence was transcribed separately. Sequences of behaviour of interacting gulls were checked afterwards to ascertain the precise timing of the changes in behaviour of the different individuals. These initial descriptions, in which most attention was paid to the position of the different parts of the body, included for each gull its postures, locomotion patterns, and short movements. For each interaction between two or more gulls the orientations and distances between each possible dyad of gulls were also noted.

In this paper the emphasis will be on the postures of the gulls. This does not necessarily imply that only the statics of the behaviour will be considered: an accurate representation of sequences of postures also reveals its dynamic properties (movement patterns). The classification of these postures was based on four criteria. Figure 1 shows how the posture in the upper right corner (repeated in each row with black heads) may vary when changes occur in each of the following components:

(1) angle of the body axis; three variants differing by 45 degrees: body axis up (a), horizontal (b), and down (c);

(2) position of the wings (see Manley 1960); four variants: wings against the body (d), carpal joints slightly away from the body (e), carpal joints far from the body (f), and entire wings extended from the body (g);

(3) position of the neck, which according to Stout & Brass (1969) and Galusha & Stout (1977) would be very important in the communication of the glaucous-winged gull; five variants: neck short (h), neck stretched and vertical (i), oblique up (j), horizontal (k), and oblique down (l); and

(4) angle of the bill axis (see Manley 1960); four variants differing by 45 degrees: bill oblique up (m), horizontal (n), oblique down (o), and vertical down (p).

These four criteria would make it possible to distinguish 240 different postures. All occurrences of a particular posture which lasted at least five video frames (0.2 s) were indicated on the time-scale. All shorter occurrences were omitted in the recording of postures; they could be scored as short movements if it was possible to identify them. Short movements were always treated separately from the basic sequences of postures. Distinguished as short movements were head-flagging, head-tossing, head-bobbing, regurgitating (feeding), swallowing (eating), pecking towards partner's bill, pecking towards partner's feathers, ground-pecking, aggressive pecking, preening, head-scratching, body-shaking, head-shaking, tail-shaking, defaecating, wing-beating, wing-scissoring, and vocalizing. In the present study, short movements were only used to find similarities between postures by determining to what extent they occurred simultaneously with these postures, and so will not be described further. The locomotion patterns, orientations, and distances will not be considered here.

Preliminary Analyses

The usefulness of the detailed classification of postures was tested by analysing ca. 4.5 h of gull behaviour recorded in April and May 1977 in different parts of a gullery. This material comprised 106 interactions of various kinds between two, or sometimes more, randomly chosen individuals, which were not further apart than three body lengths. Different interactions rarely referred to the same individuals. The method yielded about 3500 units of postures, of which I examined the frequencies and the durations. From the 240 possible categories 114 occurred at least once, 49 at least 10 times, and 17 at least 50 times. Most interactions contained a few rare categories.

This detailed classification of behaviour was suitable for investigating the properties of those postures occurring relatively often. It was not suitable, however, for a statistical analysis of complete sequences of behaviour. For a study

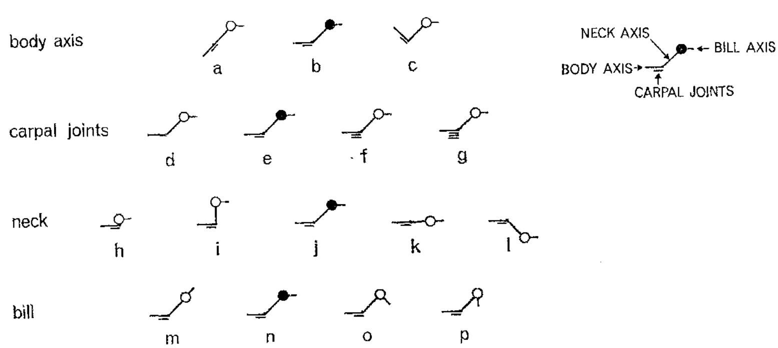

Fig. 1. Criteria used for classifying postures. The sketches b, e, j, and n are identical to the posture in the upper right (black heads). The other sketches (white heads) represent the variants of the criteria indicated on the left.

on communication it is necesary to answer at least two questions:

(1) what predictions can be made on the basis of the different behaviour patterns of an individual about the future behaviour of that individual in a given situation?

(2) what are the effects of the different behaviour patterns of the one individual on the behaviour of another individual?

Data about the sequential patterning of the behaviour (both within and between individuals) are indispensable for this kind of analysis. However, the classification of postures of the black-headed gull, as presented and used above, was hardly suitable for this purpose because many categories of postures occurred extremely seldom. I therefore decided to reduce the number of categories by lumping groups of the original categories together.

Reducing the Number of Categories

In grouping categories, it is desirable to obtain a sufficient number of groups to allow detailed description, yet each group must occur frequently enough for statistical treatment. Within each group the amount of variation with respect to form, motivation, and information content should be as small as possible.

To find the similarities between the original categories, I scored, for all 49 categories which occurred at least 10 times, as many properties as possible. The rationale behind this was that if many properties of two categories are similar, both categories should be classified into the same group. Some properties may be good guides for demonstrating similarities in motivation and information content: others may be rather poor. Since I was unable to determine the relative value of the different properties, I used as many as possible, each of which could be given a quantitative value for comparison with those of other postures. These properties fall into three groups.

(1) Properties Relating to the Occurrence of the Posture

(a) Total frequency. One might imagine that two postures (x and y) always occur in a fixed sequence (x–y) and never in other contexts. If this kind of relation exists between x and y, it is likely that the motivational factors for x and y are similar. If so, then the frequency of x should be equal to the frequency of y. Thus, similarities in the frequencies of two postures might result from similarities in motivation.

(b) Mean duration. One might imagine that two postures (x and y) can substitute for each other in all contexts in which they occur. It is then very likely that the motivational factors for x and y are similar, and that the mean durations of x and y are also similar.

(c) The relationship between observed frequency and expected frequency on the basis of random combination of the components of that posture (body-axis, carpal joints, neck, and bill). This was expressed as (observed − expected)/$\sqrt{}$(expected) for comparison between postures.

(d) Relative variation of the duration of the posture: standard deviation/mean duration.

(e) Frequency distribution over the season: percentage occurring in April.

(2) Properties Relating to the Form of Postures

For these properties scores were arbitrarily chosen. For most components, score 0 was assigned to the rest position. The scores for the variants of each component were equidistant, and because of this the absolute levels of scores did not affect the outcome after standardization (see below).

(a) Angle of the body axis: up (score + 1), horizontal (0), or down (− 1).

(b) Position of the wings: against the body (0), carpal joints slightly away from the body (1), carpal joints far away from the body (2), or entire wings extended from the body (3).

(c) Angle of the neck axis: vertical (+ 3), oblique up (+ 1), horizontal (− 1), or oblique down (− 3).

(d) Extension of the neck: short (0), or extended (1). If the neck was short, the score given for the angle of the neck axis was the mean of all scores for that property (+ 0.73).

(e) Angle of the bill axis: oblique up (+ 3), horizontal (+ 1), oblique down (− 1), or vertical (− 3).

(3) Properties Relating to the Occurrence of Short Movements

In order to find similarities, I determined for all 49 postures the frequencies (per minute) of simultaneous occurrences of the following short movements:

(a) vocalization (our material was not good enough to differentiate between the various kinds of vocalizations. They were only scored if bill movements were visible); (b) head-tossing; (c) short preening movements; (d) wing-beating; (e) aggressive pecking; (f) ground-pecking; (g) head-flagging.

In order to make comparisons between the different postures, the scores on the various properties had to be standardized. For each property the mean score became 0, and the variance 1. The following formula was used to calculate these standardized scores:

$$a_i' = \frac{(a_i - \bar{a})}{\sqrt{1/n \, \Sigma \, (a_i - \bar{a})^2}}$$

in which: a_i' = the standardized score for posture i on property a; a_i = the original score for posture i on property a; $\bar{a}$ = the mean of the original scores on property a; and n = the number of postures.

For each posture these standardized scores on all 17 properties were ranked and Spearman's rank correlation coefficients between all pairs of postures were computed. These correlation coefficients were used for classifying postures. The main trends in the correlation matrix for 49 postures are visualized by means of a dendrogram of a single-link cluster analysis (see e.g. Morgan et al. 1976) in Fig. 2. Postures which are better correlated with each other than with any other postures, are connected by small horizontal lines at the level of the correlation coefficient (indicated on the left). The level of the other horizontal lines corresponds to the highest correlation coefficient between postures in different clusters. It becomes clear from this picture that high correlations never occur between postures with large differences in form. A few groups containing strongly resembling postures can easily be detected, for instance the four postures in cluster A, the three in cluster B, the three in cluster C, the four around D, and the two near E.

For a final classification of the original postures into groups I tried to adhere to the follow-

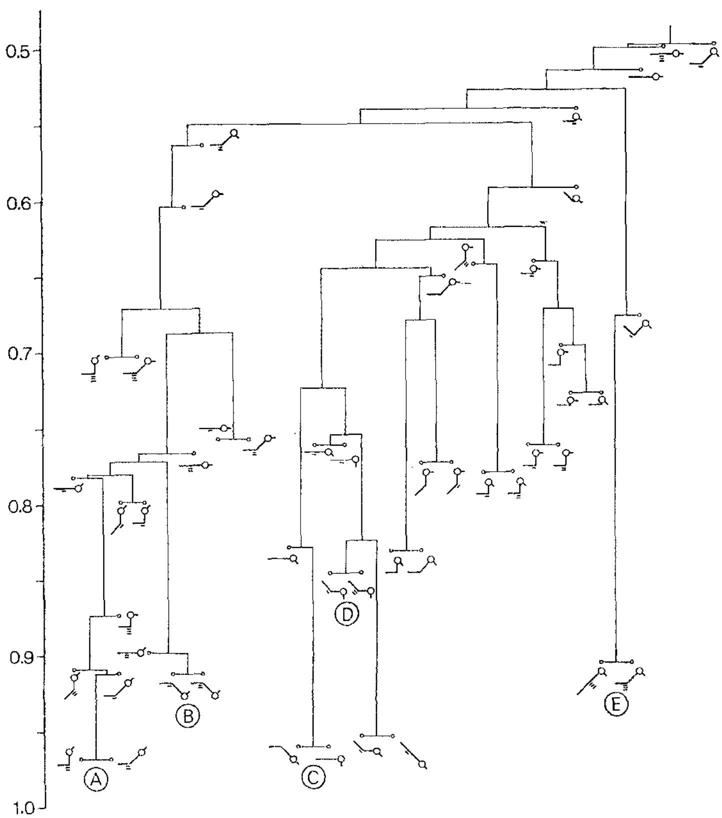

Fig. 2. Dendrogram of a single-link cluster analysis on the correlation matrix of the 49 postures. Correlation coefficients are indicated on the left. The letters A, B, C, D, and E refer to clusters of very similar postures.

ing criteria: (1) high correlations within groups, (2) lower correlations between groups, and (3) uniformity in the general features of groups.

The last point implied that I tried to compose groups with similar total frequencies. It also implied that if, for instance, there were reasons to distinguish for one set of postures between a group with wings against the body and a group with wings *not* against the body, I considered whether for other sets of postures the same distinction could be made. On the basis of these rules the 49 postures occurring at least 10 times were classified into 17 groups. On the basis of their form the 65 categories occurring less than 10 times could easily be placed in these groups.

Figure 3 gives the final composition of the different groups. Black heads refer to the most common posture in the group. These postures will be used in the following part of this paper as the most representative form of the derived categories. Grey heads refer to the other postures occurring at least 10 times, and the white heads refer to postures occurring less than 10 times. To illustrate the similarities within the groups, postures differing in only one adjacent variant of one component (body-axis, carpal joints, neck, or bill) are connected with lines. The terminology used is — as far as they are in agreement — identical to the old terminologies of gull displays. The addition of the word 'In' means 'wings against the body', and of the word 'Out', 'carpal joints away from the body'.

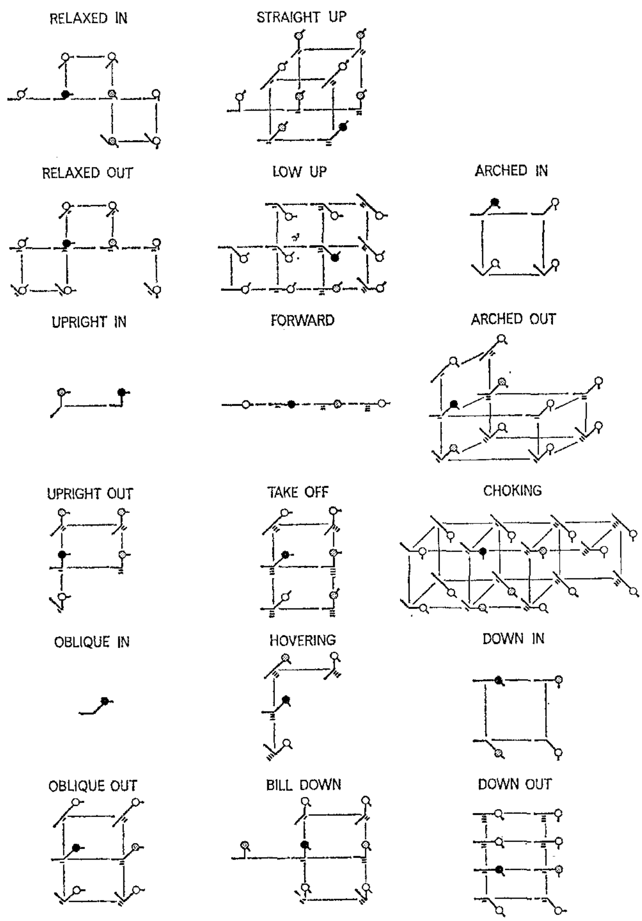

Fig. 3. Composition of the derived categories of postures. Black head: most common posture. Grey head: posture occurring at least 10 times. White head: posture occurring less than 10 times.

Comparison with Earlier Classifications

In earlier papers the emphasis was on 'ritualized displays' (see e.g. Manley 1960). These displays were distinguished from 'unritualized' postures intuitively rather than objectively. My approach to the behaviour avoids subjective bias. All postures performed by the gulls were considered. Consequently, some of the derived categories could not be equated with any of the displays recognized by Moynihan (1955), or could only be equated with the 'Normal' posture distinguished by Manley (1960). Similarities between my categories and those distinguished by Moynihan and Manley are shown in Table I.

This comparison shows that each of the postures distinguished by Moynihan and Manley corresponds, with respect to its form, in several details to one or a few categories in my classification of behaviour. Nevertheless, it has to be stressed that the different categorizations are not fully overlapping. I doubt whether identical classifications can be produced by different investigators using subjective criteria. To maximize the chance of repeatable results, a classification needs to be based on objective criteria and systematic procedures, as presented in this paper.

In the following sections an attempt will be made to compare the interpretations of the postures in the different classifications. Most attention will be paid to the Straight Up and the Low Up, because some of their properties seem to be distinct from those of the other postures.

Duration of the Derived Categories of Postures

Durations of postures may give some information about their underlying causal processes. For that reason the durations of all separate events of the different categories were measured. All sequences of the original categories belonging to the same derived category were considered as one event of the same posture. The durations of the new events were therefore identical to the durations of these sequences of original categories. On the basis of these durations I examined the relationship between the probability of ending a posture, and the duration for which the posture had already been maintained. More details about the method, in particular how it copes with the low frequencies of the longer durations of bouts, are given by van Rhijn (1977). The results are shown in Fig. 4.

If ending a bout occurred completely randomly, all graphs should be horizontal lines. Most graphs, however, show a decrease in the probability of ending. To investigate the significance of these probability changes a Chi-square test was used (two-tailed, 1 *df*) between the observed and expected (random ending of bouts) numbers of bouts above and below the mean. In seven categories the probability of ending decreases significantly (asterisks). This decrease may be related with variations in the probability with time or from one situation to another: Table II shows that for many postures the mean durations change from April to May. In four cases the change proved to be statistically significant (Mann–Whitney U test, two-tailed, $P \leq 0.05$). The decrease in the probability of ending may also be related to the fact that some postures are often performed in the course of a transition from one extreme towards another.

Table I. Similarities with Earlier Classifications

	Moynihan (1955) (Tinbergen 1959)	Manley (1960) (Tinbergen 1965)
Relaxed In	— /(Hunched)	Normal / (Hunched)
Relaxed Out	Hunched / (—)	Hunched / (Normal)
Upright In	— / (Anxiety Upright)	Normal / (Upright-2)
Upright Out	Anxiety Upright	Upright-2
Oblique In	— / (Oblique)	Normal / (Oblique-2)
Oblique Out	Oblique	Oblique-2
Straight Up	Oblique	Oblique-3
Low Up	Forward	Forward-3
Forward	Forward	Forward-2
Take-Off	—	Normal
Hovering	— / (Copulation)	Normal / (Copulation)
Bill Down	Aggressive Upright	Upright-1
Arched In	— / (Aggressive Upright ?)	Normal / (Erect Arched)
Arched Out	Aggressive Upright?	Erect Arched
Choking	Choking	Choking
Down In	— / (Choking ?)	Normal / (Low Arched)
Down Out	Choking?	Low Arched

For instance, during the transitional phase between Low Up and Straight Up (a very common transition, as will be discussed in the following sections), the gull may adopt Forward and/or Oblique Out for a second or so. The number of short events is relatively high for such postures.

The two graphs for Straight Up and Low Up suggest an increase in the probability of ending. A Chi-square test (two-tailed, 1 *df*) between the observed and expected numbers of bouts above and below the mean bout duration did not give a statistically significant result. Table III shows, however, that for both postures durations between 1.5 and 2.6 s tend to occur more often than would be expected if postures ended randomly (for Straight Up $P < 0.01$, and for Low Up $P < 0.10$; 1 *df*). It seems plausible that these postures have a typical duration of about 2 s.

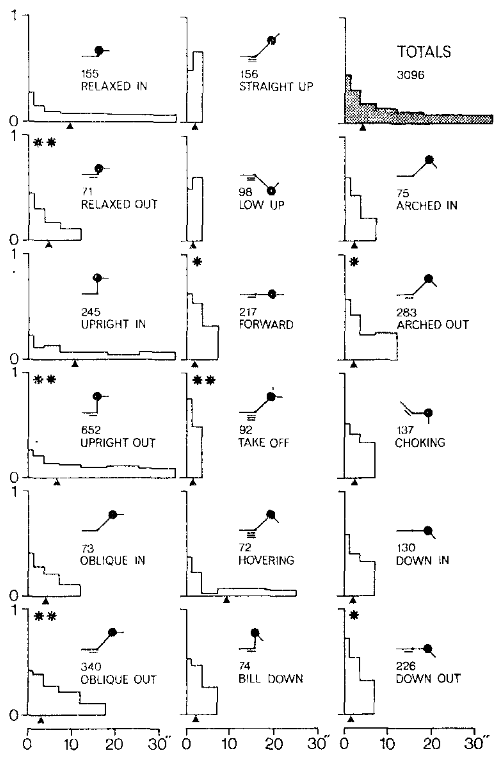

Fig. 4. Probabilities per time unit of 1.2 s (ordinate) of ending a derived-category posture, related to the time (in seconds) for which the posture is maintained (abscissas). Mean bout durations are indicated with black triangles. The number of bouts is specified for each posture. For the longer bout durations probabilities are averaged over more than one time unit. Significant deviations from the null hypothesis (constant probability, see text) are indicated with asterisks: $*P \leqslant 0.05$, $**P \leqslant 0.01$.

Why might these postures have a typical duration? From a comparison with the other postures one receives the impression that they were so difficult to perform that a gull could not sustain them for a long period. In that case the duration of these postures could provide a measure of the 'quality' or the fitness of the performer, in which case there would be reasons for the bird to sustain them for as long as possible. This would tend to lead to the probability of ending rising with bout duration.

To determine whether there are reasons for the bird to sustain the Straight Up and Low Up as long as possible, I examined the contexts in which these and other postures were shown. Table II demonstrates that the Straight Up, Low Up, Upright Up, Upright Out, Oblique Out, and Forward occur relatively often during the early part (April) of the season. Most other postures are more often performed during May. Moynihan (1955) and Manley (1960) have already stressed that the meeting ceremonies between partners consist of a sequence 'Oblique'–'Forward'–'Upright' with head-flagging. In the beginning of the season these sequences are most elaborate. In that period 'Oblique' and 'Forward' may alternate several times before the bird adopts the 'Upright' posture with head-flagging. Manley (1960) claimed that in these sequences 'Oblique' was always performed in the 'Oblique-3' variant (comparable with my Straight Up) and 'Forward' always in the 'Forward-3' variant (comparable with my Low Up). A decrease in the complexity of meeting ceremonies should therefore result in relatively high frequencies of Straight Up and Low Up in the early part of the season.

As is shown in Table IV interactions between partners also contain a considerable number of the other three postures (Upright Out, Oblique Out and Forward) which are often performed during the early part of the season. Also, a number of them frequently occur during agonistic interactions between males (B). In meeting ceremonies the emphasis is laid on Low Up; in agonistic encounters Oblique Out and Straight Up tend to predominate. The finding that this group of postures is most frequently shown during the early part of the season suggests that this behaviour is particularly important between animals which are not fully accustomed to each other. This could imply that these postures play a role in the transfer of information of the

Table II. Mean Durations (s), Frequencies (in brackets) and Percentage of Occurrence of the Derived Categories of Postures during the Early (April) and a Later Part (May) of the Season

	April			May			Mann–Whitney U test on durations	Chi-square test on frequencies
	Mean	N	%	Mean	N	%		
Relaxed In	10.6	(13)	1.2	11.5	(142)	7.0	NS	M**
Relaxed Out	3.0	(2)	0.2	5.8	(69)	3.4	NS	M**
Upright In	21.1	(26)	2.4	12.0	(219)	10.9	A*	M**
Upright Out	8.6	(323)	29.9	6.8	(329)	16.3	A**	A**
Oblique In	10.0	(14)	1.3	3.7	(59)	2.9	A**	M*
Oblique Out	4.6	(190)	17.6	2.1	(150)	7.4	A**	A**
Straight Up	2.0	(68)	6.3	2.1	(88)	4.4	NS	(A)
Low Up	2.0	(59)	5.5	2.3	(39)	1.9	NS	A**
Forward	1.7	(97)	9.0	2.8	(120)	6.0	NS	A**
Take-Off	2.1	(19)	1.8	1.8	(73)	3.6	NS	M*
Hovering	5.8	(8)	0.7	11.9	(64)	3.2	NS	M**
Bill Down	2.2	(30)	2.8	3.7	(44)	2.2	NS	NS
Arched In	3.6	(1)	0.1	2.4	(74)	3.7	NS	M**
Arched Out	2.2	(99)	9.2	2.8	(184)	9.1	NS	NS
Choking	2.5	(58)	5.4	2.9	(79)	3.9	NS	NS
Down In	2.4	(1)	0.1	2.5	(129)	6.4	NS	M**
Down Out	1.9	(72)	6.7	1.7	(154)	7.6	(A)	NS
Totals		1080			2016			

A = longer/more often in April; M = longer/more often in May; (A) $P \leqslant 0.10$; $*P \leqslant 0.05$; $**P \leqslant 0.01$.

Table III. Analysis of the Durations of the Straight Up and Low Up Postures

Duration (s)	Frequency of Straight Up			Frequency of Low Up		
	Obs	Exp	χ^2	Obs	Exp	χ^2
0.2–1.4	76	78.4	0.05	48	53.8	0.52
1.5–2.6	60	31.5	24.89 ($P < 0.01$)	30	19.9	4.63 ($P < 0.10$)
2.7–3.8	11	16.8	1.67	12	10.9	0.03
3.9–5.0	5	9.0	1.36	2	6.0	2.04
$\leqslant 5.1$	4	10.3	3.27	6	7.4	0.11
Totals			31.24 ($P < 0.01$)			7.33, NS

Two-tailed tests, 4 *df*.

Table IV. Frequency (%) of Five Postures in Males and Females in Different Situations: A = Male (with Partner), B = Male (with Male), and C = Female (with Partner)

	Situation			χ^2 comparison between:		
	A	B	C	A/C (abs)	A/C (rel)	A/B (rel)
Upright Out	23.1	18.3	19.4	A**		(A)
Oblique Out	8.8	18.3	6.3	A**		B**
Straight Up	3.1	6.3	4.7			B**
Low Up	2.4	1.1	3.5			
Forward	3.5	6.8	7.8		C**	B**
N	1215	558	825			

abs = observed frequencies should be equal (situations A and C have similar total durations); rel = observed frequencies should be proportional to total frequencies (N); situation with highest frequency is indicated: (A) $P \leqslant 0.10$; $*P \leqslant 0.05$; $**P \leqslant 0.01$; all tests two-tailed with 1 *df*.

identity and quality of potential partners or potential neighbours. This is compatible with the indication that a gull tries to sustain Straight Up and Low Up as long as possible.

Sequences of Postures

To complete the comparison between the different classifications, the order in which my categories occur must be examined. Also, an analysis of sequences might provide additional evidence for discovering situations in which the different postures occur and what kind of information could be transferred by a posture. Inclusion of the behaviour of the partner and/or opponent is certainly helpful for solving these questions.

For the analysis of sequences, all data were pooled. Sample size was not large enough to analyse the behaviour of the two sexes in different situations separately. For the sequential patterning of postures within an individual the durations of postures were not taken into account. For the sequential patterning between individuals, the behavioural change of the one individual was related to the preceding behavioural change of the other individual, if there were no other changes in between, and if the time interval between both changes did not exceed three time units (3.6 s). The criterion of three time units was chosen because it was very doubtful whether a behavioural change in the one individual occurring more than three time units later than the last behavioural change in another individual, could still be regarded as a reaction. Figure 5 shows that the highest frequencies of behavioural changes in other individuals occur during the half time units just before and just after postures start (− 0.6 up to + 0.6 s). These graphs also give an indication about how often the different postures can be related with reactions in other individuals (right halves of the graphs), and how often they can be considered themselves as reactions (left halves). It is striking that most graphs seem to be fairly symmetrical. The three upper postures in the second column (Straight Up, Low Up, and Forward) seem to be particularly strongly related with behavioural changes in other individuals.

In the contingency table of the sequential patterning of postures within an individual, the descending diagonal remained open by definition: a given posture could not be followed by the same posture. To analyse this table I used the same procedure as Slater & Ollason (1972), taking account of the zeros in the diagonal. The significant positive relationships ($P \leq 0.05$) are represented by arrows in Fig. 6. It can be seen that most relationships are reciprocal. In this diagram the areas of the circles are proportional to the frequencies of the postures.

It is worth noting that all postures with wings against the body, classified as 'Normal' by Manley (1960), are strongly clustered. The only connection with the other postures is between Arched In and Choking. It is also clear that within the behaviour complex of Oblique Out, Straight Up, Low Up and Forward, almost all kinds of transitions occur significantly more often than would be expected by chance. Upright Out is not clearly associated with this complex. Relaxed Out and Bill Down are only connected with Upright Out; Take-Off is associated with Straight Up (mainly as chasing and fleeing) and with Hovering; Hovering (the copulation posture of the male) is further associated with Arched Out; and the luring postures (Arched Out, Choking, and Down Out) are strongly interrelated.

In the contingency table of the sequential patterning of postures between individuals the

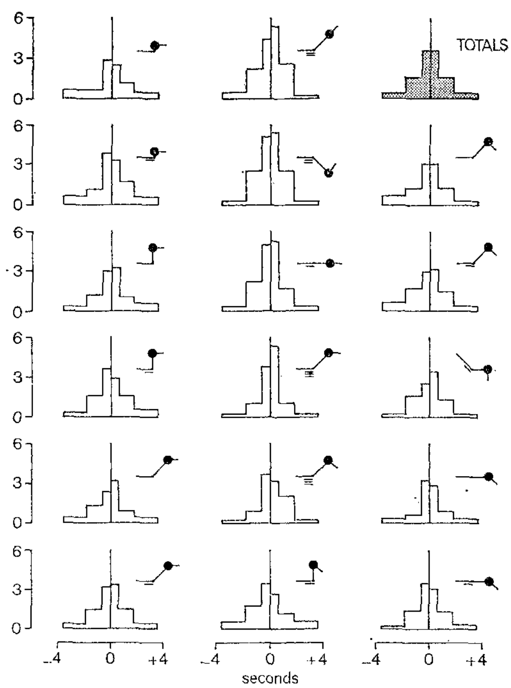

Fig. 5. Mean frequency per 10 s (ordinates) of behavioural changes in the one individual just before or just after (abscissas) the start of each of the indicated postures by another individual.

descending diagonal was not left open. I therefore first analysed this matrix using a conventional method, chi-square. This revealed that almost all postures were significantly more often followed by the same posture in another individual than could be expected by chance ($P \leq 0.05$). These postures are depicted as grey circles in Fig. 7. Relationships between similar postures may be caused by factors other than those causing relationships between different postures. It is very likely that similar external factors influencing the different individuals simultaneously more often cause relationships between similar postures than between different postures. I therefore decided to neglect the information in the descending diagonal for a study of the relationships between different postures. The procedure (Slater & Ollason 1972) was thus similar to the analysis of the sequential patterning of postures within an individual. The signifi-

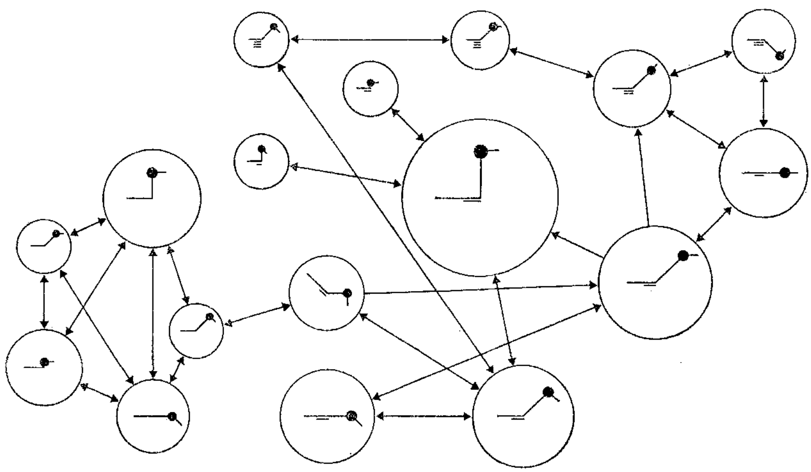

Fig. 6. Sequential relationships between postures within an individual. Arrows indicate significant positive relationships. The areas of the circles are proportional to the frequencies of the postures.

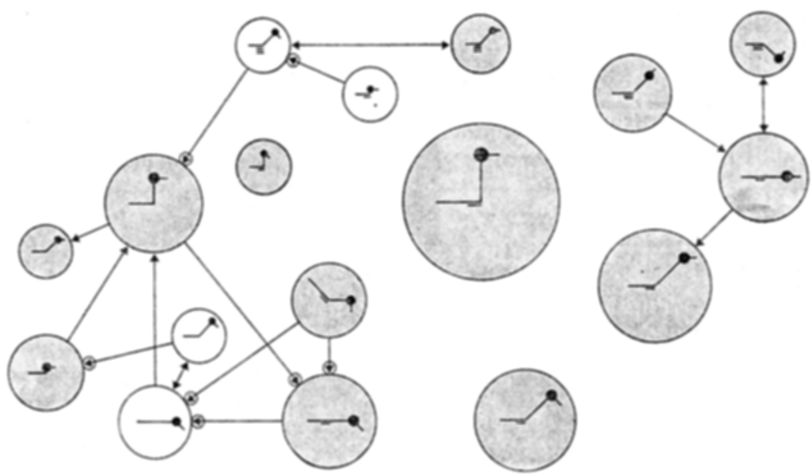

Fig. 7. Sequential relationships between postures between individuals. Grey circles indicate a significant positive relationship with the same posture. Arrows represent the other significant positive relationships. Arrows with circles refer to relationships occurring only in the sequential patterning between individuals. The areas of the circles are proportional to the frequencies of the postures.

cant positive relationships ($P \leq 0.05$) are represented by arrows in Fig. 7. Relationships shown by the arrows with small circles are unique for the sequential patterning between individuals: the other arrows were also found in the sequential patterning within individuals (Fig. 6).

The postures with wings against the body are still fairly well interrelated. Three of them (Relaxed In, Upright In, and Oblique In) are associated with the same posture in the other individual. The number of connections with other postures is higher than in Fig. 6. Upright In is performed as a reaction to Hovering, which can be interpreted as the response of a not fully receptive female to a copulation attempt of a male. The finding that Upright In is often followed by Down Out can be related to the start of luring by a male of a female (Upright In). The arrows from Choking and Down Out to Down In are associated with the fact that luring (Choking) and regurgitation (Down Out) in the male evoke swallowing (Down In) in the female. The finding that all three luring postures (Arched Out, Choking, and Down Out) are associated with the same posture in the other individual, indicates that they are also performed in non-luring contexts (e.g. agonistic encounters). The arrow from Relaxed Out to Hovering is related to head-tossing and the copulation posture of the female (Relaxed Out) evoking a copulation attempt by the male. In the Oblique Out–Straight Up–Low Up–Forward complex, all postures are depicted as grey circles, indicating that different individuals perform these postures synchronously. The lack of connections between the most extreme postures of this complex (Straight Up and Low Up) is in accordance with this synchronization.

Returning to the idea that Straight Up and Low Up are used for the transfer of information about the quality of the performer, the sequential patterning of postures may provide a means for this information to be assessed. Firstly, an individual performs both postures in alternation, both during a meeting with its (potential) partner and during an aggressive encounter. In meeting ceremonies the number of repetitions of both postures decreases as the pair bond becomes stronger (Manley 1960). Secondly, between individuals the performance of both postures seems to be perfectly synchronized. Upon closer inspection there may be slight differences in the durations of postures between individuals. If the duration for which these postures can be sustained is a measure of the quality of the performer, these synchronized ceremonies might offer an opportunity for a bird to estimate the quality of its partner or opponent in comparison to its own quality (see Zahavi 1977). Thus, the Straight Up–Low Up ceremony of black-headed gulls could be analogous to the roaring of the red deer (Clutton-Brock & Albon 1979). For the black-headed gull the ceremony could help to select the best partner, and to find a site in the colony with neighbours of similar fighting capacities.

Concluding Remarks

The objective method for categorizing postures presented in this paper resulted in a more detailed classification of behaviour of the black-headed gull than did the earlier intuitive ones (Moynihan 1955; Manley 1960). The Normal posture was divided into a number of categories, and the variants of Upright, Oblique, Forward, and Arched could be described as basically different postures. Definitions in my classification were not fully overlapping with earlier definitions.

On the basis of the present classification two postures (Straight Up and Low Up) differed from the others in form, duration, and in the context in which they occurred. These unique properties led me to the hypothesis that these postures are used to transfer information about the quality of an individual during a stage when individuals are not fully known to each other (see van Rhijn 1980; van Rhijn & Vodegel 1980). I want to remark that these unique properties could not be derived from Manley's classification, because Straight Up was, in a large number of cases, taken together with Oblique Out, and Low Up with Forward. This hypothesis, which has to be further tested, could throw some light on the problem of transfer of information about resource holding potential and about intentions (see Parker 1974; Maynard Smith 1979) in the first and subsequent confrontations between individuals.

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