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CAUSATION AND FUNCTION OF DIFFERENT VOCAL REACTIONS OF LITTLE GULLS LARUS MINUTUS TO INTRUDERS NEAR THE NEST

by

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1. Introduction

For many decades, the communication behaviour of gulls and terns has been a subject of study by ethologists. As a result, the visual and vocal display repertoire of a great number of species has been described (CULLEN, 1956, 1957; MANLEY, 1960; MOYNIHAN, 1955, 1956, 1958; STOUT et al., 1969a and b, STOUT, 1975; TINBERGEN, 1953, 1959). Although visual behaviour patterns have been given much more attention than vocal ones, general descriptions of vocalizations are available for many species. These usually include vocalizations referred to as 'Attack' and 'Alarm Calls', which are said to be associated with overt attack and escape behaviour. However, this association has never been quantitatively demonstrated.

During a study of the communication behaviour of the little gull, *Larus minutus*, in a breeding colony in the Netherlands, observations revealed that far more than two types of vocalizations may be heard during interactions characterised by overt attack and escape behaviour. Moreover, call types intuitively categorised by us as Attack and Alarm Calls, upon closer look, seemed less rigidly associated with overt attack and escape behaviour than first expected. These observations have led to a more

thorough investigation of the way in which vocalizations are used by little gulls during agonistic interactions, carried out in the 1983 breeding season. This paper describes (1) what kind of vocalizations occur during agonistic interactions, (2) how these vocalizations are related to attack and escape behaviour and (3) whether individual birds behave differently under similar external conditions. Finally, problems of causation and function of vocal communication during agonistic interactions are discussed.

2. Material and methods

Observations for this study were collected in the period April-July 1983 in the Lauwersmeer area, the Netherlands. A description of the study area and the little gull population is given by VEEN (1980).

Agonistic interactions were defined as any interaction between little gulls during which either overt attack behaviour was shown, or overt escape behaviour which could be regarded as an effect of aggression by the other bird. Agonistic interactions occurred at all stages of the breeding cycle, *i.e.* in the pre-laying, the incubation and the chick-rearing period. In the pre-laying and chick-rearing period, the situations in which agonistic in-teractions took place were extremely varied, including encounters in a pair formation con-text (both in the air and on the ground), rivalry on gathering places and disputes over chicks wandering in a neighbouring bird's territory. As a rule such interactions were ac-companied by a variety of postures and calls. They usually took place at large distances from the observer, while the participating birds were not individually recognizable. In contrast, agonistic interactions in the incubation period nearly always consisted of en-counters between nesting birds and intruders in the breeding territory. Such interactions could be observed at close distance, the nesting birds could be individually identified and the communication behaviour recorded almost exclusively consisted of vocalizations. We restricted our observations to this period, because interactions were less complex than in the early part of the season. Besides conspecifics, a variety of other bird species were recorded as intruders in little gulls' nesting territories. The behaviour of the nesting birds shown in reaction to the latter seemed rather similar in comparison to conspecifics. Therefore, non-conspecific intruders were included in the observations as well.

Two small breeding colonies, consisting of 6 (colony A) and 15 (colony B) pairs, were selected for detailed study. Colony A was situated in an open grassland plain. In the beginning of the season the area was extremely wet and the little gulls all started to nest on a slightly higher ridge. As a consequence all nests were situated in a row. Distances be-tween nests varied between 3 and 50 m. A few black-headed gulls *Larus ridibundus*, com-mon terns *Sterna hirundo*, avocets *Recurvirostra avosetta*, a black-tailed godwit *Limosa limosa* and a redshank *Tringa totanus* nested in the neighbourhood of the little gulls. Colony B was situated on dryer ground, covered with a mixed vegetation of grasses, herbaceous plants and some small willow trees, part of which grew up rather high, reaching a height of about 50 cm in the course of the season. Nests were at distances of 2-15 m and the little gulls were surrounded by several nesting common terns, black-headed gulls and, at a distance of a hundred meters, herring gulls *Larus argentatus*.

All observations were made from blinds, placed on platforms 1.2 m above ground level, at distances between 20 and 100 m from the birds. In order to be able to distinguish be-tween individuals, some birds were colourmarked with dyes (picric acid and Rhodamine B) by means of remote controlled drop-bottles, mounted on a stick placed near the nest.

The visual communication behaviour was observed through binoculars with magnifica-tions varying from 10-25 ×. Observations were written down or recorded on tape.

Vocalizations were recorded on a Uher 4200 tape recorder and a Sony TC D5M cassette recorder, using Sennheiser omnidirectional (MKH 105) microphones placed in the field. Visual and vocal behaviour was recorded synchronously on a portable JVC videorecorder (HR 2200) with a Philips camera (VK 4000, lens 75 mm). If possible, spoken comments were recorded on tape together with video and sound records.

Vocalizations have been analysed on a Uniscan I (type 4500) Spectrum analyser (range 0-10000 Hz) which displays frequency/time and time/amplitude sound spectrograms on a monitor, where frequency, time and amplitude can be measured to the nearest 160 Hz, 0.018 sec and 1 dB, respectively. Frequency/time hard copy sound spectrograms were produced on a Kay Sona Graph model 6061 B, using wide band (300 Hz) filter setting.

3. Results

3.1. Observations under natural circumstances.

In order to study what kind of vocalizations can be heard during agonistic interactions of little gulls and how these might be related to attack and escape, our first approach was to do observations under natural circumstances. In colony A, between 28 May and 19 June data were collected on nine different days during which three little gull's nests were kept under continuous observation for periods varying in length from 5 to 8 hours. The behaviour of birds intruding in the nesting territories as well as the reactions of the nest owners were recorded.

Altogether, five different call types were made by the nest owning little gulls during the interactions. A typical frequency/time spectrogram of each is given in Figure 1. The call types distinguished all consist of a varying number (1 up to more than 20) of sound figures, which we shall refer to as notes. Call types were classified on the basis of temporal, frequency and amplitude characteristics. Duration of notes and intervals between notes were the major criteria for discrimination. Two call types, namely Eeyit and Whèt appeared to be characterized by a highly specific pattern of frequency modulation as well. Sometimes intermediate forms between call types were recorded (Tuk/Keè, Keè/Whèt and Eeyit/Whèt). In such cases calls were allocated to one of the types on the basis of a quantitative analysis of the spectrogram.

The vocal reactions of the nesting little gulls to intruders, expressed as the total number of notes per call type, have been determined for interactions with different intruder species. The latter have been grouped in (A) conspecifics, (B) non-conspecifics which pose no threat to the little gulls and (C) non-conspecifics which can be regarded as potential predators on the little gull or its brood. The results are summarized in Table 1. Tuk, Keè, Whèt and Eeyit were recorded in reaction to a variety of predator species, whereas Kay was only heard in reaction to conspecifics and to a common tern. Comparison of the data for the different groups of in-

truders distinguished, for the minimum distance at which the nests were
approached, and for intruders appearing on foot and in flight, did not
reveal differences by which the frequency of occurrence of Tuk, Keè,
Whèt and Eeyit could be explained. We also could not find consistent dif-
ferences in the vocal reactions of little gulls which were sitting on their
nests or flying (not indicated in the table).

Since it was likely that the type of call during the agonistic interactions
was determined by aspects of the behaviour of intruder and/or nest owner
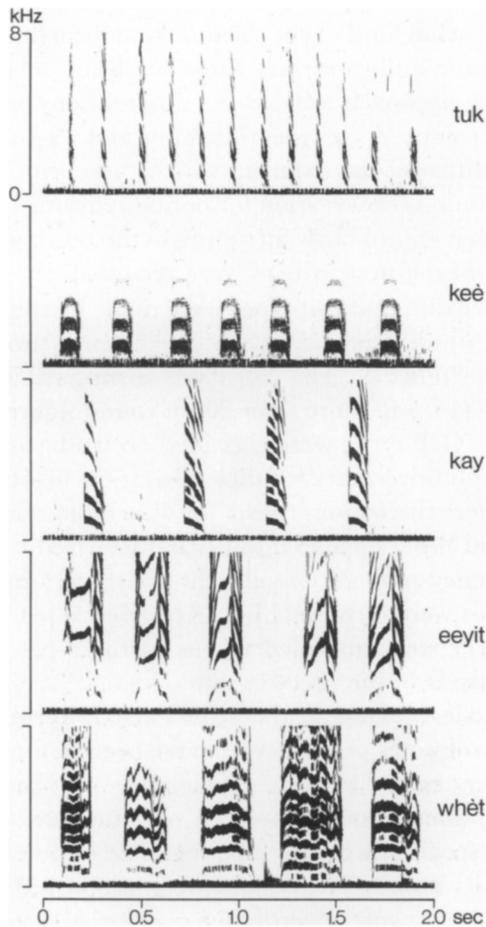

Fig. 1. A typical frequency/time spectrogram of the five call types given by little gulls dur-
ing aggressive interactions.

BLE 1. Vocal reactions (total number of notes recorded for each call type for all eractions) of the little gulls to different bird species intruding in the breeding territory under natural circumstances

Intruder species	Inter-actions (n)	Way of approach	Minimum distance to nest (m)	Reactions by little gulls (number of notes)				
				Tuk	Keè	Whèt	Eeyit	Kay
little gull	9	on foot	0.5	119	27	9	15	19
common tern	3	on foot	0.2	77	59	19	27	7
ruff	5	on foot	0.1	51	108	11	20	0
avocet	1	on foot	1	10	0	0	0	0
redshank	1	on foot	2	0	0	0	1	0
shelduck	2	on foot	0.8	5	0	0	5	0
oystercatcher	3	on foot	3	10	12	103	6	0
grey heron	2	in flight	30	0	0	0	6	0
black-headed gull	15	on foot	0.5	109	80	9	82	0
herring gull	27	in flight	20	78	35	0	152	0
marsh harrier	15	in flight	25	66	369	1	46	0

e number of interactions, the way of approach of the intruder and the minimum intruder-nest distance orded, is indicated. A = conspecific, B = intruders which can be regarded to the harmless, C = predators.

which remained hidden during observations under natural circumstances, we decided to do experiments in which the behaviour of the intruder could be controlled.

3.2. Experiment I: Placing a motionless intruder in the territory.

During the interactions under natural circumstances the behaviour of the intruder usually changed constantly. Moreover, if the intruder was a predator, several breeding birds might react at the same time. This made it extremely difficult to determine how the vocal behaviour of the little gulls was related to the situation. To be able to study the behaviour of the gulls in a more standardized situation, an experiment was conducted in which a stuffed conspecific intruder was placed near the nests.

On 21 June two tests of 15 minutes duration were carried out in colony B with a stuffed adult little gull placed at 1 m from the nearest nests. After the model had been positioned, the observer walked to the blind which was situated at 50 m distance from the nests under observation. To preclude that the data comprised reactions of the breeding birds to the presence of the observer in the colony, observations were started 2 minutes after the observer had entered the blind. During the experiment

the visual and vocal behaviour of little gulls reacting to the model was recorded on video. When the observations were started, the breeding birds nearest to the stuffed gull always circled above the model and attacked by diving at it. Although most little gulls returned to their nest during the test period, at least one individual continued its attacks on the model until the end of a test. Sometimes two or more gulls attacked the model almost simultaneously. To preclude that our data comprised interactions between little gulls simultaneously present above the model, observations of reactions by single birds were selected for analysis. All vocalizations recorded were attributed to one of four phases of the attack flight: (A) circling above the model, (B) diving at the intruder, (C) attacking the intruder at the lower point of the swoop and (D) moving upward and away from the model.

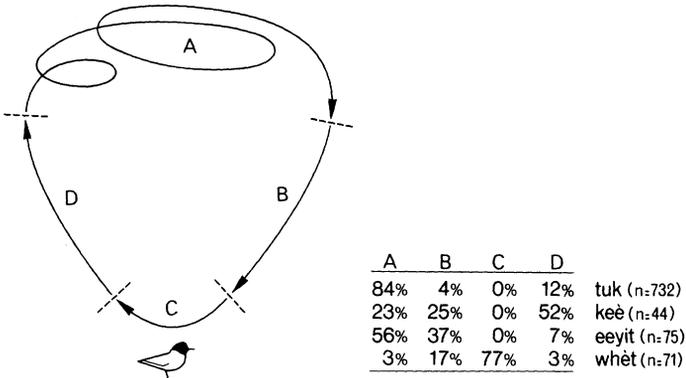| A	B	C	D	
84%	4%	0%	12%	tuk ($n = 732$)
23%	25%	0%	52%	keè ($n = 44$)
56%	37%	0%	7%	eeyit ($n = 75$)
3%	17%	77%	3%	whèt ($n = 71$)

Fig. 2. Generalized flight path of little gulls attacking a stuffed conspecific intruder placed near the nests, and the frequency distribution (% notes) of Tuk, Keè, Eeyit and Whèt for different stages (A, B, C and D) of the flight path.

The results of the experiment are summarized in Figure 2. Tuk, Keè, Eeyit and Whèt calls were recorded in reaction to the model. Tuk notes were mainly given when the birds circled. Keè notes were relatively most common when the gulls moved away from the model. Eeyit notes mainly occurred when circling above the model and during a downward swoop. Since the amount of time spent by the birds in stage A was relatively large and because the majority of Eeyit calls recorded in this stage occurred immediately before the transition to stage B, Eeyit can be regarded to be strongly associated with the moment of starting a diving attack. Finally, Whèt notes occurred most frequently at the lowest point of the attack.

3.3 Experiment II: Reactions to movable intruder models.

Whether and how little gulls react to intruders in the nesting territory can be expected to depend on (1) the species of intruder, and (2) its distance to the nest. Moreover, individual birds can be expected to react differently. To study the influence of the above mentioned aspects on the tendency of a nesting bird to fly up, to attack and to vocalize, an experiment was conducted in which the models (a stuffed juvenile little gull and a stuffed adult black-headed gull) could be moved towards and away from the nests.

In colony A blinds were erected in front of two groups of nests, one with two nests 8 m apart and another with three nests 4-5 m apart. All individuals belonging to the experimental nests could be recognized individually. From inside the blind, using ropes and pulleys an intruder model mounted on a small green sledge was pulled from under a cover in a straight line from 15 m distance towards a nest (Fig. 3). As soon as the incubating little gull flew up from its nest, the model was pulled back. The model was moved at constant speed as much as possible. Trials lasted 2 minutes on average.

During the trials the position of the model and the behaviour of the nesting gull were recorded by two observers. Simultaneously with spoken comments, the vocalizations of the experimental bird were recorded on tape. If possible, five trials with intervals of at least 10 minutes were done in succession with the same individual on a particular nest. Sometimes, a series of trials was interruped because nest-relief took place. As a consequence some series of trials had to be completed on different days. Trials during which more than one bird reacted to the model were excluded from the analysis. Altogether 42 trials with the little gull model and 31 with the black-headed gull model were conducted between 7 and 18 June, including 9 and 5 individuals respectively at 5 nests.

Distance and intruder species.

The behaviour of the nesting birds during the trials was as follows: when the model started its approach, the birds reacted with alert behaviour (neck stretched, looking around). At shorter model-nest distances they flew up from their nest, circled around above the model and usually attacked. After some time, when the model was on its way back, the breeding birds alighted again on their nest.

Similar to the previous experiments, four call types were given by the nesting little gulls: Tuk, Keè, Eeyit and Whèt. Fig. 4 summarises the
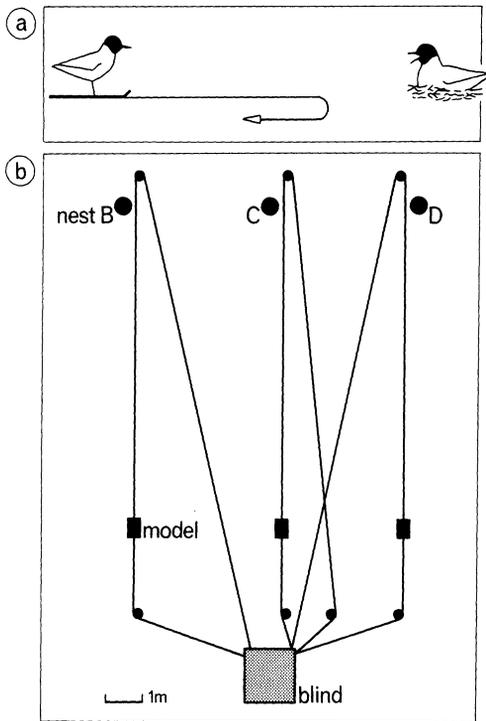
Fig. 3. Set up of the experiment in which movable stuffed intruders were pulled towards and away from incubating little gulls. (a) Schematic side view of stuffed little gull on sledge approaching and incubating bird and (b) ground-plan showing position of nests, hide, ropes and pulleys.

reactions of five little gulls, which were tested under similar conditions with both the little gull and the black-headed gull model. The figure gives for each call type the average number of notes per bird per second at different distances, while moving the stuffed little gull towards and away from the nests. The number of attacks at different distances is given at the bottom of the figure. Distances are related to the turning point of the model, which was determined by the moment at which the incubating birds flew up from their nests.

The figure shows marked uni- en bimodality of curves. The course of the graphs indicating the average number of attacks shows marked conformity with those indicating the average number of Whèt notes. The occurrence of Whèt and Attack thus seems positively correlated. The reverse is true for the average number of attacks and the average number of Tuk notes, since the graphs indicating Tuk show a marked trough
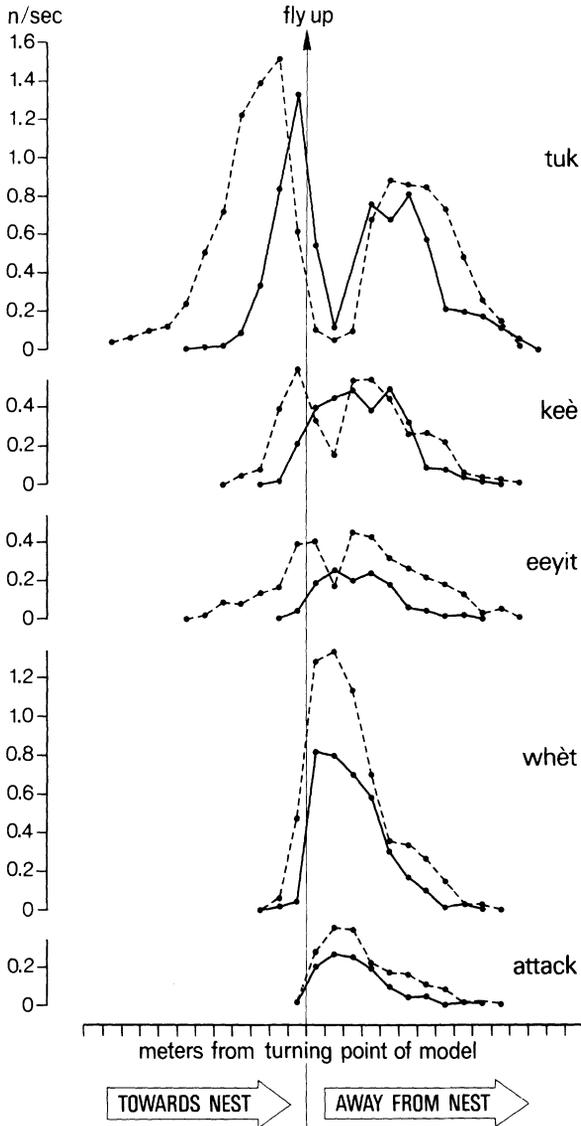
Fig. 4. The average number of notes (for Tuk, Keè, Eeyit and Whèt) and attacks per second given by five litlle gulls reacting to stuffed conspecific (solid line) and black-headed gull (broken line) intruder models pulled towards and away from the nests. Distances are related to the point at which the incubating birds flew up from their nests and the model was pulled back. Number of trials: little gull model n = 24, black-headed gull model n = 31. Further explanation in text.

when the number of attacks reaches a peak. As far as the relationship with attack is concerned, Keè en Eeyt show positions intermediate to Whèt and Tuk: in the experiment with the little gull model the graphs for Keè en Eeyit both take a course which shows similarity with the graph indicating attack, but in the experiment with the black-headed gull model in the graphs for Keè and Eeyit a trough is apparent coinciding with a peak in the frequency of attacks, as was found for Tuk.

At the beginning of the approach phase only Tuk notes were given, at shorter distances Keè + Eeyit appeared and, finally, also Whèt. When the models were pulled away from the nests, disappearance of the call types occurred opposite to the order of appearance. As a consequence of the fact that the data for all trials were aligned with the moment of flying up, the point at which the gulls returned to their nests cannot be indicated in the figure: it fell between 3.3 and 10.0 meter of the model's way back (average 6.0 m from flying up point). Without exception, Eeyit and Whèt notes had completely disappeared once the birds returned to their nests. There was a noteworthy number of Keè notes given by birds moving from above the model to their nests, whereas a small number of Tuk notes was still given by the birds after they had settled again.

A comparison of the reactions to the little gull and the black-headed gull model shows that the breeding birds, on average, reacted at greater distances (see Tuk, Keè and Eeyit) and also more strongly (see frequency of Tuk, Eeyit, Whèt and attack) to the black-headed gull than to the little gull. In addition, the nesting gulls flew up and alighted at greater model-nest distances in case of the black-headed gull model as compared to the little gull model (average scores for black-headed gull and little gull model: fly up 3.2 *vs* 1.5 m, alight 10.2 *vs* 6.5 m).

Figure 4 suggests specific relationships in the frequency of occurrence between call types and attacks. However, at this point it should be stressed that the results presented in the figure only give an overall picture of how the nesting gulls reacted to the models. Since there was considerable variation in the reactions obtained in different trials, an analysis whether and how vocalization and attacks are interrelated should preferably be done by comparing their coincidence per trial. To this end a Kendall Rank correlation test was applied comparing the total number of attacks and the number of Tuk, Keè, Eeyit and Whèt notes occurring in each of 42 trials done with the little gull and in 31 trials done with the black-headed gull model. (All individuals (n = 9) tested with the little gull model were incorporated in this analysis, in contrast with Fig. 4 which only includes the data of individuals (n = 5) tested with both types

of dummies). The results are presented in Fig. 5. For trials with the little gull model, positive correlations are found between attack on the one hand and Keè, Eeyit and Whèt on the other, between Keè-Whèt and between Whèt-Eeyit. Negative relationships exist between attack-Tuk, Tuk-Whèt and Tuk-Keè. If we now consider the correlations found for the trials with the black-headed gull, attack is again positively correlated with Eeyit-Whèt and negatively correlated with Tuk. However, Keè is no longer positively correlated with attack. Instead, a negative but non-significant correlation exists. Keè is also negatively correlated with Whèt. It thus comes out, that the correlation between attack and Keè is different
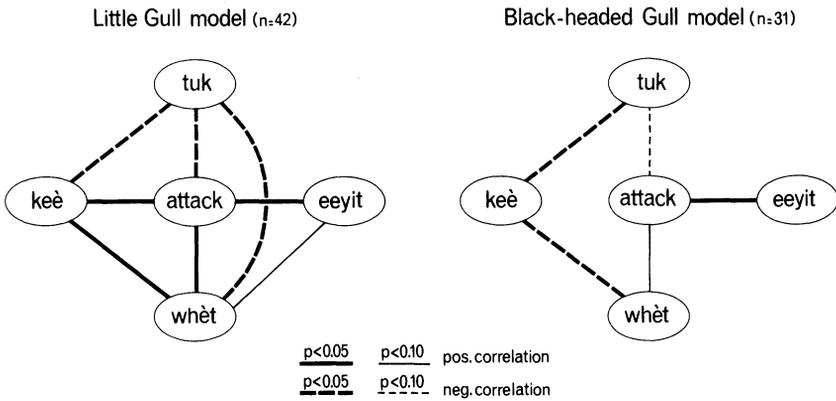

Fig. 5. Statistically significant correlations (10% level) in the occurrence of attack, Tuk, Keè, Eeyit and Whèt in tests with the little gull (above) and the black-headed gull (below) model. Kendall Rank Correlation test, two-sided, p values indicated in figure. Further explanation in text.

for trials with the little gull and the black-headed gull model. How can this be explained? Fig. 4 showed higher attack frequencies to the black-headed gull than to the little gull. Moreover, it showed differences in the course of the graphs indicating the frequencies of Keè and Eeyit to the two types of models: the graphs indicating frequencies of Keè and Eeyit given in reaction to the little gull model roughly ran parallel to the graph indicating frequency of attacks, but in the graphs for Keè and Eeyit heard in reaction to the black-headed gull, a marked dip was recorded when average frequencies of attack were highest. Apparently, an increase of the frequency of attacks above a certain level occurs at the expense of Keè and, to a lesser extent, Eeyit. This phenomenon logically results in a decrease of the strength of the positive correlation between attack on the

one hand and Keè and Eeyit on the other, once attack frequencies exceed
a certain level and, eventually leads to a change in the relationship from
positive to negative with further increase of the frequency of attacks.

The correlations between the occurrence of attack and the four types of
vocalizations seem, in part, contradictory to what one would expect from
the results obtained in experiment I (section 3.2, Fig. 2). The occurrence
of Tuk when circling and Whèt at the lowest point of a downward swoop
are in agreement with the positive correlation between attack and Whèt
and the negative correlation between attack and Tuk. But, experiment I
suggests a positive correlation between attack and both Eeyit and Keè, ir-
respective of the frequency of attacks, since Eeyit and Keè were given
during the approach and the withdrawal phase, respectively, and these
phases are an inseparable part of each single attack dive. However, the
height from which attack dives were started, and consequently the length
of the approach and withdrawal phase, was negatively correlated
with the frequency of attacks ($r = -0.35$, $p < 0.05$, $n = 253$, equation
$y = -1.91x + 3.04$ where y is the height at which attack dives start and x is
the number of attacks per second). This means that an increase of the at-
tack frequency (and Whèt) resulting in a relative decrease of Keè and
Eeyit, is not necessarily in conflict with the relationship between vocal
types and flight path phase as shown in experiment I.

Summarizing, we conclude that the experiment with the movable
models has shown that the occurrence of the various call types heard dur-
ing agonistic interactions depend on distance and species of intruder.
Call types are associated with attack in different ways; the strongest
association exists between attack and Whèt, followed by Eeyit, Keè and
Tuk.

Individual variation.
It has been emphasized before that marked differences existed in the at-
tack frequency and the relative frequency of the four types of vocalizations
between different trials. To investigate whether and to what extent this
might be the result of differences between individuals, the data for birds
tested with the little gull model ($n = 9$) have been analysed separately.
Comparison of the data of individual birds gives a reliable picture of
inter-individual differences only if such differences cannot be attributed
to variation in the conditions under which individuals were tested.
However, in spite of variation in testing conditions (such as differences in
intervals between trials; eggs or chicks in nest), we always found a
remarkable constancy in the reactions of individuals. In series of suc-

cessive trials no signs of habituation were found. Trials with the same individual at different days also yielded remarkably similar reactions. Fig. 6 presents the reactions of an individual which was tested on 15 and 18 June, when there were eggs and chicks in the nest, respectively. Even in
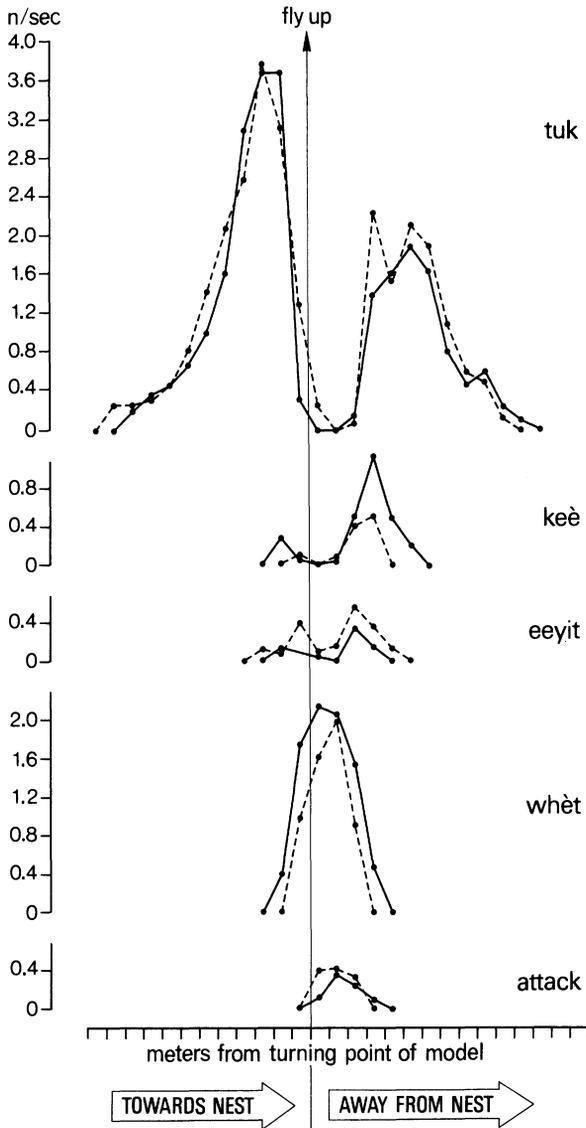

Fig. 6. Reactions of a nesting little gull to an intruder model (stuffed black-headed gull) presented when there were eggs (solid line) and chicks (broken line) in the nest. For further explanation see subscription to figure 4 and text.

these situations surprisingly similar reactions were obtained. In contrast
to the great intra-individual constancy, marked inter-individual variabili-
ty in the reactions to the models was recorded. Fig. 7 gives the data for 3
individuals, demonstrating the great range of variation existing.

To investigate the existence of inter-individual variation for all birds
tested, we determined per individual: (1) the average flying up and
alighting distance, (2) the average number of attacks per minute over the
period when the bird was in the air, (3) the average number of notes per
minute (irrespective of call type) over the whole period a trial lasted, and
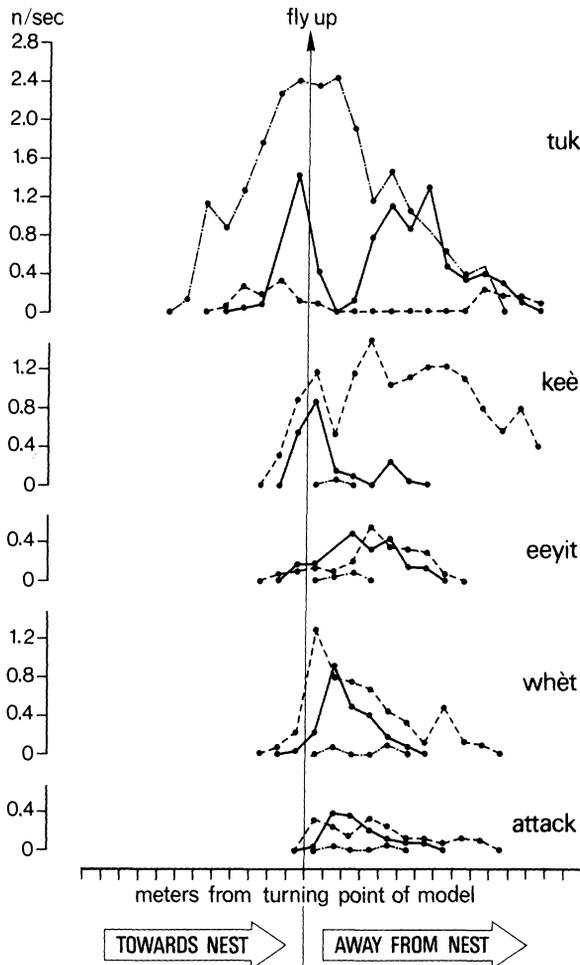

Fig. 7. Reactions of 3 individual little gulls to a conspecific intruder model showing inter-
individual variation. For further explanation see subscription to figure 4 and text.

(4) the average number of Tuk, Keè, Eeyit and Whèt notes per minute over the whole period of a trial, expressed as percentage of total number of notes.

There was significant inter-individual variation for all variables measured (Kruskal Wallis analysis of variance, $p < 0.01$ for all cases).

Marked individual differences were found with respect to number of attacks and relative frequency of different call types (Fig. 8). An extremely high proportion of Tuk notes was given by birds 8 and 9. Keè notes were often recorded in bird 7 and were also relatively frequent in birds 3

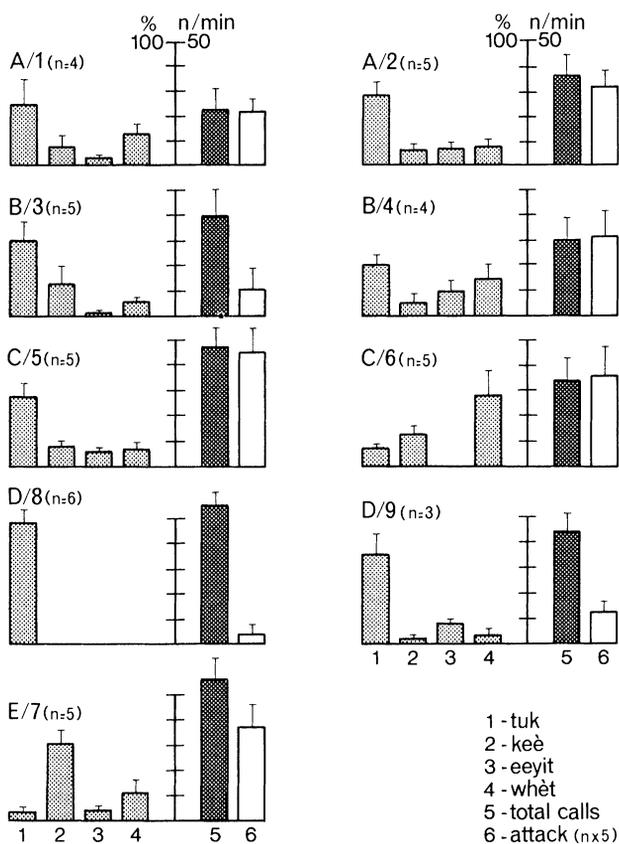Fig. 8. The average number of Tuk, Keè, Eeyit and Whèt notes per minute expressed as percentage of total number of notes per minute, and average number of attacks and calls (total notes) per minute for individual little gulls reacting to movable stuffed conspecific models. Capitals near graphs indicate nests, numbers refer to individuals, sample size is number of trials, + 1SE indicated at top of bars.

and 6. Eeyit was commonly uttered by birds 2, 4 and 9, whereas a remarkably high proportion of Whèt calls was present among the reactions of bird 6.

Considering the occurrence of the various call types in relation to attack, Fig. 8 shows that a relatively low attack frequency (birds 3, 8 and 9) coincides with a relatively high frequency of Tuk. However, between individuals having a relatively high attack frequency (birds 2, 4, 5, 6 and 7) the pattern of occurrence of Keè, Eeyit and Whèt is variable and no specific correlation of these calls with attack seems present: To verify this general impression and to compare the results obtained for different trials (see Fig. 5) with those for individual birds, a Kendall Rank correlation test was carried out on number of attacks and number of vocalizations for individuals. The results showed the expected negative correlation between attack and Tuk ($p < 0.01$, two-tailed), but also a positive correlation between attack and Whèt ($p < 0.01$, two-tailed).

The marked individual variation in the occurrence of different call types can be explained to a great extent by individual differences in the tendency to attack. However, other factors contribute to individual differences as well, such as differences in the tendency to give only one or a prolonged series of notes of a particular call type in a particular situation. For instance, in the air during the approach phase of a diving attack, the average number of Eeyit notes per individual varied between 1 and 4. Similar differences were recorded for Keè and Whèt. Finally, individual differences were also recorded for type of vocalization given in a particular situation. For instance, bird 7 often gave Keè notes in situations in which Tuk was given by the other birds. Bird 9 almost exclusively uttered Whèt notes at the lowest point of a diving attack as well as during the approach phase when Eeyit was given by most other birds.

Summarizing, we conclude that there are marked individual differences in the way vocalizations are used during agonistic interactions. Differences concern both the frequency of occurrence in a particular situation as well as the relationship between type of vocalization and type of situation.

4. Discussion

4.1. Causation.

The causation of displays during agonistic interactions has often been explained as an attack-escape or an approach-avoidance conflict, *i.e.* as a consequence of the simultaneous activation of two counteracting motiva-

tional systems (TINBERGEN, 1959; MOYNIHAN, 1955; BAERENDS, 1975; VODEGEL, 1978). Recently, the hypothesis that the performance of displays corresponds with a particular motivational state and, consequently, will provide information about the internal state of the performer, has repeatedly been criticized by investigators applying game theory to animal contests (see *e.g.* MAYNARD SMITH, 1982). Despite this criticism, we wish to consider the causation of the behaviour of the little gulls described in this study as a consequence of motivation and shall attempt to explain the behaviour of the gulls in terms of an attack-escape conflict. This choice is based on the following functional reasoning: (1) An intruder which threatens a little gull's territory or brood is likely to activate the gull's attack motivation (abbreviated as A), since attack seems the most effective behavioural response to avert this kind of danger. (2) An intruder which poses a threat to the adult little gull itself, either because it is a predator or, in case of a conspecific intruder because a fight may result in injury, is likely to activate the escape motivation (abbreviated as E). Escape seems to be the most appropriate behavioural response to avoid being attacked.

The gull's movements in relation to A and E.

In our experiments, the incubating little gulls nearly always reacted with frequently attacking the model. We are of the opinion that, because of the occurrence of overt attack behaviour, the attack motivation of the reactor must have been activated by the intruder model. However, in nearly all trials, immediately after they had flown up from their nests, the incubating birds hovered or circled above the model. In case of the conspecific model, flying up occurred when the intruder was, on average, at a distance of 1.5 meter from the sitting bird, whereas the distance between model and reactor was 8.0 meter on average when the latter circled above it. This means, that the incubating birds, in first instance, moved away from the model. Besides, two individuals (birds 8 and 9) kept on circling above the model in a number of trials. These observations lead us to conclude that an escape motivation must have been activated by the intruder as well. As a rule, circling above the model and attacking it both occurred in the same trial, sometimes with intervals of only a few seconds. Moreover, many intermediate forms of the two behaviours were recorded, such as shallow dives during circling, high above the model. These observations are in favour of the assumption that the attack and escape motivations were simultaneously activated.

MILLER (1971) found in rats that the tendency to approach and to avoid a stimulus both increased with decreasing distance from the stimulus. Similar results have been obtained by VODEGEL (1978a, b) who studied the agonistic behaviour of the Cichlid fish *Pseudotropheus zebra*. According to MILLER, the tendency to avoid a stimulus is more affected by distance than the tendency to approach, so that their gradients intersect at a particular distance from the stimulus. By either approaching or avoiding the stimulus each individual would strive to reach and stay at the distance where both tendencies are equal. MILLER's model and the way in which it has been exended by VODEGEL are largely applicable to our data on the little gull. With decrease of distance between model and incubating bird A and or E can be expected to increase until either of the two tendencies exceeds the bird's tendency to incubate the eggs. It then flies up and initially shows avoidance behaviour, which is in agreement with the view that E is affected more than A.

But how can we explain an individual's subsequent attack on the model? Studies on habituation (see *e.g.* HINDE, 1970; VODEGEL, 1978a, b) have shown a negative relationship between the time that a stimulus is presented and the strength of A and E. Moreover, VODEGEL has provided evidence that E decreases faster than A. In case of our little gulls, during circling, the above mentioned effect of habituation on A and E would result in E becoming weaker than A, which could explain the initiation of a diving attack. A decrease of the distance to the model, when diving at it, will then lead to an increase of A and E, until E, which is supposed to increase faster (see MILLER's statement above), exceeds A. At this point the attacker turns away from the model until it again reaches a distance where A and E are of equal strength.

During the experiment with the movable model, the little gulls always returned to their nests when the model was pulled back. However, the distance between model and nest at which the gulls alighted was significantly greater than the distance at which they flew up (see section 3.3), which seems rather surprising if a distance effect on A and E determines whether an individual leaves the nest or not. At this point it should be stressed that, during the experiment, the behaviour of the gulls can be expected to be under the influence of motivational factors other than A and E, which may interfere with the latter. All little gulls tested incubated a clutch and a tendency to incubate might constantly be in conflict with A and E. Since there is evidence that the tendency to incubate is positively influenced by tactile stimuli resulting from contact with the eggs (BAERENDS, 1970), the threshold for A and E set by this tendency, can be

expected to be higher for an incubating gull than for a flying individual. This may explain the difference observed in flying up and alighting distance.

A comparison between the trials with the little gull and with the black-headed gull model (section 3.3) revealed that vocal reactions and attacks were more often seen to the latter than to the former. As far as the attack frequency is concerned, this seems contradictory to the results obtained by VODEGEL (1978a, b), who found a marked decrease of the relative frequency of attacks with increasing model size, whereas the time spent performing agonistic displays increased. Although our data are not directly comparable to her's, they indicate neither an absolute nor a relative decrease of overt attack behaviour on the larger sized black-headed gull. To our opinion, this can be explained by differences in the kind of models employed in both studies. VODEGEL presented to her fishes conspecific dummies of different sizes, which were intruders and potential sex partners at the same time. In our study, the little gull and the black-headed gull model should be regarded to have acted as intruders only. This may have accounted for more attacks on the larger-sized black-headed gull. An increase of the number of attacks on the black-headed gull model, if compared with the little gull model, can also be explained because black-headed gulls are predators on the brood of the little gull.

Vocalizations in relation to A and E.

In the foregoing, flying up and alighting, as well as the movements of the little gulls in the air, have been explained as a result of variation in the absolute and relative strengths of A and E as functions of time (habituation) and of distance between model and reactor. Different vocalizations have been shown to occur at different distances from the intruder model and were related to flight direction (Figs 2 and 4). This makes it possible now to relate these vocalizations to A and E (Fig. 9). Tuk notes were mainly given by individuals on the nest at the beginning of the approach of the model and, by birds in the air, during circling. For both situations it has been argued that A and E must be relatively weakly activated and of about equal strength. At shorter distances between reactor and intruder model, on the ground as well as in the air, Keè and Eeyit notes dominated. A and E both increase with decrease of distance and the strength of these tendencies thus can be expected to be higher for Keè and Eeyit than for Tuk. However, in the air Eeyit almost exclusively occurred when the model was approached, whereas Keè was mainly given when

the birds moved away from the model. This implies that A must be stronger than E in case of Eeyit and weaker in case of Keè. Finally, Whèt almost exclusively occurred at short distances between model and incubating birds and at the lowest point of a diving attack. It has been argued that, because of the distance effect on A and E, these situations are characterized by relatively high levels of activation of A and E, with both tendencies about equal in strength.
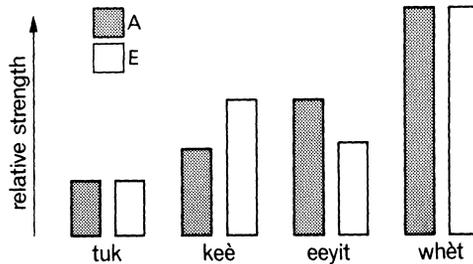

Fig. 9. Supposed relative strengths of A and E for situations in which different types of vocalizations are given during agonistic interactions. Further explanation in text.

An analysis of our data at the individual level (section 3.3) showed marked differences in the frequency of occurrence of different call types. To a large extent these differences could be related to differences in the behaviour of individuals, such as the tendency to circle above an intruder or to attack it and, consequently, to interindividual differences in the strength of A and E. Similar results have been obtained by VODEGEL (1978), who was able to relate the occurrence of displays during agonistic interactions of individuals of *Pseudotropheus zebra* to the individuals' relative aggressiveness or A/E ratio. However, we also found differences in the type of vocalization given in similar situations: one bird often gave Keè during circling, *i.e.* in situations in which Tuk was given by other birds. Another bird almost exclusively uttered Whèt notes at the lowest point of a diving attack as well as during the approach phase when Eeyit was given by most other birds. We had the impression that these differences were correlated with the distance from the intruder at which individual birds started their attacks. For instance, attack dives might be launched from such a short distance, that the approach phase was practically equivalent to the lowest point of the attack. In such cases Whèt often occurred in the approach phase. Similarly, the occurrence of Keè during circling seemed dependent of the distance to the intruder at which

circling occurred. For practical reasons we were not able to measure details of the way in which diving attacks were performed by the different individuals. Therefore we are unable to provide data to verify the explanation suggested above.

Call structure in relation to A and E.

In the literature, a relationship has been suggested between the physical structure of a display and its underlying motivational state (for visual displays, see TINBERGEN, 1959 and BAERENDS, 1975; for vocalizations, see MORTON, 1977 and 1982, and ZAHAVI, 1982). This makes it interesting to consider the physical structure of Tuk, Keè, Eeyit and Whèt in relation to the underlying strengths of A and E as suggested above. In Fig. 1, for each call type, sonagrams have been presented. It appears, that the various call types distinguished show marked differences with respect to note duration, interval duration and frequency modulation. In the order Tuk-Keè-Eeyit-Whèt note duration strongly increases, which coincides with an increase of the presumed attack motivation. Eeyit and Whèt show marked frequency modulation. Both call types are supposed to be related with a high absolute and, in case of Eeyit, also with a high relative attack motivation. The strength of A thus might be related to both note duration and frequency modulation.

4.2. Function.

In the previous section it has been suggested, that the various call types of little gulls which can be heard during agonistic interactions are related with different strengths of motivational systems for A and E. If this is correct, each call type can be expected to give information about the sender's tendency to attack or to escape. However, it has been stressed before, that a range of strengths of the motivational states rather than a specific state is likely to be the causal factor underlying each call type. This will strongly decrease the calls' predictive value.

During agonistic interactions Tuk is given in situations characterized by a relatively large distance between reactor and intruder. Tuk is not immediately preceded or followed by actual attack. Moreover, individual birds which exclusively utter Tuk have not been recorded to attack. Apart from an agonistic context, Tuk is also given by little gulls alighting on their nests in undisturbed situations, such as after a defaecation flight in between two incubation stints or while bringing nest material to the mate at the nest. The occurrence of Tuk in an agonistic as well as in other

contexts might be explained by assuming that it gives information of the sender being alarmed, and functions in warning neighbouring individuals, mate and young. In the agonistic context, as a result, chicks may hide in the vegetation and neighbouring birds may join in defending the colony area if the intruder is a predator. When alighting on the nest, a warning may prevent the sender from being attacked by the mate or a neighbour which is approached unnoticed. Tuk notes are characterised by a relatively low amplitude, also when the intruder is still at a large distance. This is in agreement with the view that this vocalization is intended for receivers at short distance, *i.e.* neighbouring birds and relatives at the nest. Observations under natural conditions and during experiments in which Tuk was played through a loudspeaker placed in the colony, showed that Tuk is reacted to with alert behaviour (stretching of neck and looking around), which further supports the idea of a warning function.

Eeyit notes are exclusively given during agonistic interactions and are often followed by actual attack. Under natural conditions, intruders usually react to Eeyit with avoidance behaviour. To test, whether the intruder's reactions influence the likelihood that Eeyit is followed by attack, experiments have been done in which stuffed intruders were either pulled further towards the nest or pulled back after the Eeyit notes of an incubating little gull. The results showed, that ignoring the signal always led to being attacked, whereas immediate retreat never did so. In situations in which intruders enter a little gull's territory, Eeyit given by the territory owner apparently carries the message: 'I shall attack, if provoked'. Eeyit notes are characterised by high amplitude over a large frequency range and marked frequency modulation. These characteristics make that the call penetrates over a long range, while the sender is easily located (MARLER, 1955, 1959). Eeyit seems, in first instance, to be intended for the intruder, though marked effects on neighbouring birds, such as alert behaviour, have been recorded as well.

Whèt is exclusively given by little gulls at the lowest point of a diving attack or by birds sitting on their nest reacting to persistent intruders approaching very closely. Reactions to Whèt are largely similar to those to Eeyit and may include immediate withdrawal or other avoidance behaviour, such as sitting hunched or swerving flight. The relatively high number of intermediate forms between Eeyit and Whèt also suggest resemblance of function. However, as a result of its high amplitude and long note duration, Whèt may have a stronger distraction effect on the

intruder. Since Whèt is so closely correlated in time with the actual attack, reactions to Whèt and to attack are difficult to separate.

For the functional significance of Keè no suggestion can be made at this moment.

Finally, some remarks should be made with respect to the occurrence of call type Kay, which was recorded during aggressive interactions under natural circumstances in reaction to conspecifics and to a common tern, but which was never heard during the experiments with the stuffed intruders. The functional significance of Kay has been subject of detailed study and playback experiments have shown that Kay makes little gulls individually identifiable (VEEN, 1985). Both the conspecific intruders and the common tern referred to above were breeding birds of the small colony A. (The common tern nested only a few meters away from the nearest little gulls). Communication about individual identity between breeding birds thus might be the reason why Kay was recorded in these cases and not during the interactions with other non-conspecific intruders and in the experiments.

Summary

This study deals with (1) which vocalizations are made by little gulls (*Larus minutus*) during agonistic interactions and (2) how these are related with overt attack and escape behaviour.

Under natural circumstances, when little gulls react to intruders approaching the nests, five different call types can be heard. Four of these, Tuk, Keè, Eeyit and Whèt, often occurred during experiments using stuffed intruder models (little gull and black-headed gull). Reactions of incubating little gulls to a stuffed conspecific placed near the nests, showed that the occurrence of different call types is related to different phases of the flight pattern, such as circling above the intruder, approaching, attacking and moving away. Reactions to a stuffed little gull and black-headed gull which were moved towards and away from the nests revealed that the call types Whèt, Eeyit, Keè and Tuk, were, in decreasing order, associated with actual attack. Consistent individual differences existed in the reactions to the experimental intruders.

The movements and the vocalizations made by the gulls when reacting to the experimental intruders are explained as a consequence of a conflict between motivational systems for attack and escape. It is argued that different call types are related with different strengths of activation of these systems. Differences between individuals in the reactions to the intruders can largely be explained by individual-typical differences in motivation. A comparison of the physical structure of each type of vocalization in relation to its underlying motivational state, shows a positive relationship between call duration and attack motivation. Tuk is believed to function as a warning for neighbouring birds, chicks and the mate. Eeyit seems to convey 'I shall attack, if provoked' and is intended for the intruder. Whèt probably acts as a vocal part of the actual attack and may help in impressing and distracting the intruder. The functional significance of Keè is as yet unknown.

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