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VOCAL COMMUNICATION IN GULLS AND TERNS

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Introduction

No one will doubt that birds do communicate by means of body postures, movements and vocalizations. Yet, our knowledge of the kind of information conveyed is extremely poor. The main reason for this lack of knowledge is the problem of how to distinguish between cause and effect when individuals participating in communication either simultaneously or in succession act as 'sender' and 'receiver' and thus constantly influence one another, and how to determine the way and extent to which reactions depend on context, such as time or place of occurrence, the participant's social status and relationship. As a result the study of animal communication is characterized by much speculation and theoretical consideration and a lack of penetrating field studies which provide the relevant data necessary to support theory.

Until recently it appeared almost impossible to monitor the behaviour of both sender and receiver during the communication process. However, recent development of audio-visual registration techniques have been of great help in solving this problem. Although this has also introduced the new problem of how to select the relevant data out of a wealth of information, it has no doubt led to results which might lead to a better understanding of the problem of communication. This contribution aims to give an idea of the kinds of methods used and the results obtained in the study of vocal communication of Gulls and Terns.

Gulls and Terns are social animals; they live in open terrain and concentrate in colonies in the reproductive season. In spring pair formation takes place and territories are established which are fiercely defended against conspecifics. Within the territory eggs are incubated and chicks are raised. Throughout the breeding season encounters with strangers, neighbours, mate and young frequently take place. Communication behaviour invariably accompanies such encounters. Gulls and Terns are thus almost ideal animals for a study of communication and have already been subject of such studies in the early days of ethology (Tinbergen 1953, Cullen 1957, Moynihan 1955, Manley 1960).

Vocal repertoires

Describing a Gull's vocalizations and determining measurable units is the first step to be taken. In case of the Little Gull, a species intensively studied at the Zoological Laboratory of Groningen University, vocalizations of known individuals made in different situations have been recorded in the field. Sound records were converted to spectrograms which were then analysed with respect to duration, frequency, amplitude and harmonic spectrum. The results showed that the vocal repertoire of the Little Gull consists of five units of uninterrupted sound which will be referred to as notes (Fig. 1, top). As a rule, notes do not occur on their own, but are ordered in series, termed call-types.

VOCAL COMMUNICATION IN GULLS AND TERNS

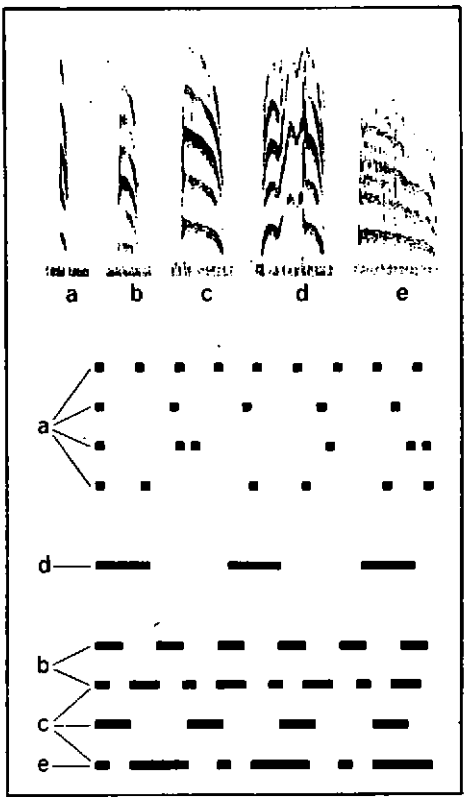

Fig. 1. Sonograms of the five elements (notes) of which Little Gull vocalizations are composed and the temporal pattern in which notes are ordered in series (call-types).

Such series are composed of one or two note-types arranged in a specific temporal pattern. Altogether, 13 different call-types have been distinguished, 9 of which are shown in figure 1.

At present, the vocalizations of a number of Gull and Tern species have been analysed in a way similar to that of the Little Gull. The species so far studied appeared to have a vocal repertoire with a temporal structure which is basically similar. The physical characteristics of notes, the total number of call-types and details of the call-type structure, however, vary from species to species.

Species recognition

The vocal repertoires of different species usually show marked differences. In contrast, differences between vocalizations of closely related species may be

extremely small and difficult for the human ear to distinguish. Common and Arctic Tern are such closely related species whose vocal repertoires as well as visual behaviour patterns and morphological characteristics are markedly similar. Since the two species often nest in the same colonies, whereas mixed pairs have never been recorded, the question may be raised how these birds recognise conspecifics. Experiments in which Common and Arctic Terns were attracted by stuffed individuals of both species have suggested that morphological features do not play a major role in species recognition (Dirksen, unpubl.). Observations on the visual communication behaviour of the two species (Cullen 1956, 1960, Schenk, unpubl.) have revealed differences which are unlikely to play an important role in species recognition either. A comparison of vocalisations, however, has shown that there is one call-type which shows marked differences in fundamental frequency, duration, amplitude and frequency modulation. This call-type appeared to be especially common during the early stages of pair formation and experiments have shown that reactions to it are highly species-specific. These results suggest direct selection pressure for distinction between particular calls in order to promote species recognition.

The Long Call, a compound message

The various call-types distinguished in the Little Gull (Fig. 1) usually occur on their own or follow each other in one out of various different ways. The Long Call seems to be an exception to this rule, for it is a combination of up to three call-types (Kay, Ke-kè and Ke-koô in figure 2) linked together in a very specific order. An example of its most extensive form is given in the figure, but abbreviated forms in which either the second or the third part is absent also occur.

Long calls are given in a number of circumstances: (1) in the air during encounters in the beginning of the breeding season when birds of different as well

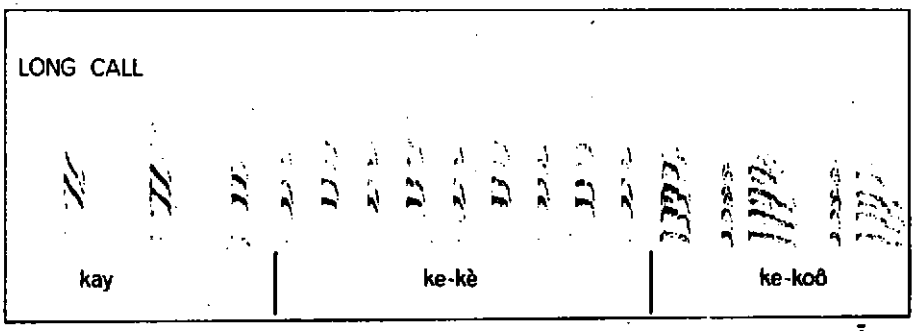

Fig. 2. Sonogram of a Long Call of the Little Gull showing tripartition. Total duration 5 secs, frequency range 0-8000 Hz.

VOCAL COMMUNICATION IN GULLS AND TERNS

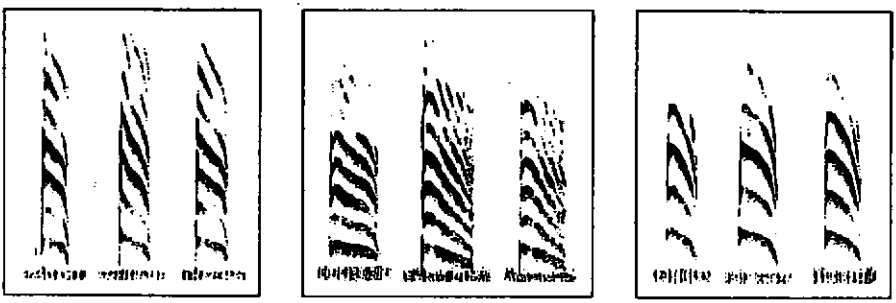

Fig. 3. Sonograms of Kay notes of different individuals showing variation in note duration, fundamental frequency, frequency modulation and amplitude of harmonics. For each individual notes were selected from different call-types.

as the same sex meet one another, (2) during encounters on the ground when pair formation is in an advanced stage, (3) during encounters between mates on the nest and (4) during encounters between parents and chicks.

In the various situations in which Long Calls occur, reactions may vary from peaceful approach followed by courtship displays or feeding of the young to flying away or even fierceful attack. This great variability may explain why so many different, sometimes apparently contradictory, functions have been attributed to it by earlier workers (such as individual or territory advertisement, long-distance threat or luring). It may therefore be questioned, whether the different parts of which the Long Call is composed might serve different communicative functions.

Apart from being the introductory notes of the Long Call, series of Kay notes frequently occur on their own and an investigation of the situation in which they occur might thus give more specific knowledge about the information conveyed. However, Kay notes appeared to be present during encounters in the air, on the ground, on the water, in as well as outside the breeding season, while foraging, and during courtship and aggressive encounters. Kay notes thus occur in nearly all situations in which vocal communication takes place and, therefore, can be expected to carry a very general message. Inspection of sonograms showed that Kay notes are highly variable and variation turned out to be individual-specific (Fig. 3). In order to test whether Little Gulls themselves recognise each other's Kay notes under natural circumstances, an experiment was conducted in which Kay notes of known individuals were played from a loudspeaker between the nests of the incubating mate and an incubating neighbour. Only mates reacted to the calls showing behaviour typical for an incubating bird immediately before it is relieved on the nest. These results lead us to conclude that Little Gulls, by giving Kay notes, make themselves individually recognizable. The variation of situations in which Kay notes are given, stressed the possible importance of individual recognition in establishing social relationships within the breeding colony as well as in feeding flocks.

VOCAL COMMUNICATION IN GULLS AND TERNS

The interesting results obtained by playback experiments with Kay notes have stimulated continuation of the experimental approach. Ke-kè notes, either alone or in combination with Kay notes, were played to incubating individuals as mentioned above. Combinations of the two notes elicited even more and somewhat different reactions than Kay notes alone, whereas Ke-kè notes alone did not cause any reaction at all. This suggests that the second part of the Long Call carries information which, in the situation in which it was tested, was of relevance to the incubating individuals only if accompanied by the caller's individual label.

Long Calls invariably occur in approach situations. Therefore, Long Calls with different compositions have been analysed with respect to distance of approach. Figure 4 clearly demonstrates that distances are relatively small when Ke-koô notes are included in the call. Ke-koô notes are mainly given in encounters with an adult of the other sex and are accompanied by postures in which elements considered to have an appeasement function can be recognised. As a consequence Ke-koô notes are believed to convey the bird's intention to approach peacefully to a short distance. Ke-kè notes might announce approach more generally and at greater distances.

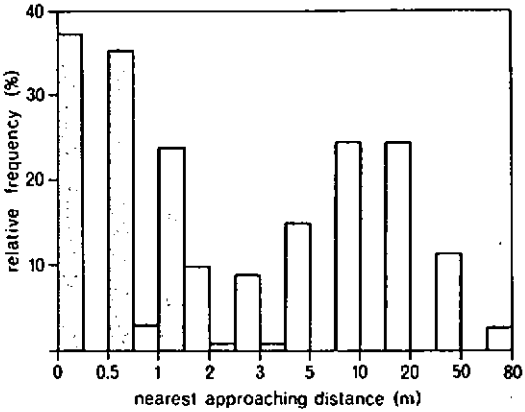

Fig. 4. Nearest approaching distance (non-linear scale) during aerial display for Little Gulls uttering complete Long Calls (hatched bars, n=419) and Long Calls missing the Ke-koô part (open bars, n=69).

Considering Long Calls as a compound message proclaiming both individual identity and the intention to approach does not explain why so often only one individual bird responds to this call. Beer (1975) has shown that Laughing Gull chicks respond differentially to playbacks of Long Calls of their parents dependent of whether these calls had been recorded during interactions with other adults or with their own chicks. Differences in amplitude made it possible to distinguish between two different Long Call types on sonogram. In the Little Gull Ke-kè notes of Long Calls recorded during encounters with strangers, mates and chicks have been shown to be different as well. Further experiments, however, are needed to unravel the way in which such differences might contribute to differences in the reactions of different categories of birds responding.

VOCAL COMMUNICATION IN GULLS AND TERNS

Information about the tendency to attack

The assumption that displays might give information about a bird's internal motivational state is well known from the classical studies of Tinbergen and his co-workers (Tinbergen 1959, Moynihan 1955, Manley 1960). As a logical consequence of the idea that displays originate from a conflict between tendencies to attack and to escape, communication behaviour was considered to give information about the probability to attack or retreat. Tinbergen (1959) divided the visual communication behaviour of gulls in 'distance-increasing' and'distance-reducing' displays.

Recently, the hypothesis that displays give reliable information about intentions has repeatedly been critisized on evolutionary grounds, applying 'game theory' to animal contests (Maynard Smith and Parker 1976, Maynard Smith 1982). However, the method used leads to answers which strongly depend on the kind of assumptions made, such as whether or not individual recognition between contestants takes place (Van Rhijn and Vodegel 1980). Therefore.the problem of whether and under what conditions displays do give information about intentions should be solved by careful observations on the animals themselves.

In the Little Gull a number of call-types often coincide with either attack or retreat. One of these, tentatively called 'Attack Call', usually occurs when either conspecifics or predators intrude in an already occupied territory. Although this call is frequently given immediately before and during attack, it may also occur in situations in which it is not at all associated with attack behaviour, suggesting that it is not a very good predictor of a bird's intentions to forcibly chase away the intruder. However, a more proper look at situations in which Attack Calls are given shows that the intruder's reactions strongly influence whether or not actual attack will follow.

To test this, an experiment was conducted in which an artificial intruder (stuffed conspecific) mounted on a sledge was slowly pulled to an incubating Little Gull. At a certain distance, the sitting bird started to react by uttering Attack Calls. Thereupon, if the model continued its approach, the sitting bird would invariably fly up and attack. If, however, the model was retrieved, the incubating bird remained on the nest and soon stopped calling. Although there was some individual specific variation in reaction distance, all individuals tested reacted in a similar way. Since we could not find differences in reactions between the experimental and the natural situation, it is concluded that an incubating Little Gull gives reliable information about its intentions to attack intruders in the territory.

Conclusion

A study of vocalisations of Little Gulls has shown that the vocal repertoire of this species is composed of only a small number of vocal elements which, in different combinations, play a role in communication. Evidence has been put forward for information about the probability to attack in one call-type (Attack Call) and a combination of information about individual identity and the intention to approach, eventually to a close distance, in another (Long Call). The Long Call of the Little Gull has been given much attention. Yet, the many dif-

ferent reactions to this call are still poorly understood.

A comparison of species has revealed that the number of call-types varies from 7 to 13. This is not a very great number, but most call-types occur in combination with different elements which play a role in communication as well. Moreover, combinations of vocalizations and postures may be embedded in behaviour sequences in a variety of different ways. This makes it extremely difficult to discern the messages conveyed and to elucidate how meaning depends on context. Therefore, it is not surprising that we are far from understanding the whole range of possible functions fulfilled by vocalizations in gulls and terns. However, a first step has been taken in an attempt to solve a fascinating problem.

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