How Do Black-Tailed Gulls Respond to Long-Call Displays of Other Individuals?

ARTICLE *in* ORNITHOLOGICAL SCIENCE · DECEMBER 2010

Impact Factor: 0.28 · DOI: 10.2326/osj.9.109

2 AUTHORS, INCLUDING:

Shinji Yabuta

Teikyo University of Science

14 PUBLICATIONS **79** CITATIONS

Ornithol Sci 9: 109–114 (2010)

ORIGINAL ARTICLE

How do Black-tailed Gulls respond to long-call displays of other individuals?

Shinji YABUTA[1,#], Hiroko KAWAKAMI[1] and Akira NARITA[2]

[1] *Department of Animal Sciences, Teikyo University of Science & Technology, 2525 Yatsusawa, Uenohara, Yamanashi 409–0193, Japan*
[2] *Aomori prefectural Hachinohe School of the Deaf, 6–29–24 Kashiwazaki, Hatinohe, Aomori 031–0081, Japan*

ORNITHOLOGICAL SCIENCE

Abstract Displays of animals do not always elicit equivalent responses from other conspecifics. Considerable variation exists among the responses, but the mechanism causing the variety remains unclear. We investigated how Black-tailed Gulls *Larus crassirostris* respond to long-call displays of other individuals. Results show that the response varies depending on the context. Territorial birds often respond to the long-calls of non-territorial birds by attacking. However, non-territorial birds typically respond to the long-calls of territorial birds by avoiding them. Nevertheless, they usually respond to the long-calls of their partners by using the same long-call. These results are explained well by the motivational conflict hypothesis.

Key words Colony, Communication, Display, Gulls, Motivation

Animals involved in social interactions often perform highly stereotyped behaviours or displays. Displays are considered to serve as signals, that is they function to alter the behaviour of other individuals (Dawkins & Krebs 1978), typically conspecific individuals. Individual reactions to displays, however, are not always the same; in fact, they vary considerably. For example, threat displays, which are considered to compel other individuals to stop approaching or retreat, often elicit attacks from opponents (Enquist et al. 1985). Furthermore, some threat displays are used not only in agonistic contexts but also in non-agonistic contexts, such as during greeting and courtship rituals (Yabuta 2002, 2008). As one might expect, the reaction depends on the context, and that begs the question: What mechanism causes such variety in response? The answer remains unclear.

The long-call display is a common display among birds in the genus *Larus* (Tinbergen 1959). Such species typically breed in colonies at very high densities; individuals form monogamous pairs and defend the small area surrounding their nest as their own territory. During the breeding season, they perform the long-call display very frequently. This display is considered to serve two behavioural purposes: as an aggressive territorial display and as a vocal greeting display between partners (Danchin 1991).

Individual responses to long-calls varies considerably (Tinbergen 1959; Veen 1987). To gain some insight into the causal mechanism of the responses demands systematic and quantitative research of that variety of responses. When a bird performs a long-call, there are usually several other birds nearby, each of which may be the target and each of which may respond. However, in the field it impractical to observe simultaneously the behaviour of all of the birds surrounding a long calling individual. Therefore, we video recorded the social interactions of Black-tailed Gulls *Larus crassirostris* at their colony and later analyzed the videos to examine how gulls responded to each other's long-calls.

In our discussion, we attempt to explain our results based on the motivational conflict hypothesis (Hinde 1970; Baerends 1975; McFarland 1993). This hypothesis suggests an explanation for the causation and evolution of displays: many displays originally arose from the conflict between the motivational systems for aggression and escape and the same motivational conflict is still the cause of the displays that are performed now.

This hypothesis assumes that that the motivational

(Received 18 December 2009; Accepted 8 June 2010)
Corresponding author, E-mail: shinji@ntu.ac.jp

systems for aggression and escape are activated when an animal encounters a conspecific (including rivals, pair partners, potential mates, parents, and offspring), although the levels of activation may differ greatly in degree. Which activity actually appears depends on the relative degrees of activation of the respective systems. If the aggression system is activated sufficiently more than the escape system, then the individual will attack; if the reverse is the case, then the individual will escape. However, if both systems are activated equally, then a system conflict occurs and the individual will display. The motivational conflict hypothesis is supported by the ambivalent nature of displays, as demonstrated through analyses of the form, behavioural sequence, and situation of many displays (e.g. Tinbergen 1959; Baerends 1975; Veen 1987). The hypothesis has also been supported experimentally, when the stimuli triggering each system have been manipulated (Blurton-Jones 1968).

METHODS

1) Field observations

The Black-tailed Gull is endemic to east Asia. We observed gull behaviour in a breeding colony at Hachinohe, Aomori Prefecture, Japan (40°32′N, 141°56′E, 2 m above sea level) during June 2007. Our study area was located 20–30 m away from Kabu-shima (Kabu island). Our observation period coincided with the post-hatching season of the gulls in this area (Narita & Narita 2004). Like other gulls, Black-tailed Gulls also perform a long-call display, the context and sequential details of which have been described in some detail (Narita 1997, 1998). In our observation area (37 m^2) eight pairs cared for their chicks and defended small territories around their nests. We marked each of the eight pairs (16 birds) with dark brown human hair dye so as to be able to identify them individually. Other, non-territorial birds sometimes visited the area for short durations. The adult gulls in the area were therefore classified as either territorial or non-territorial birds. The former were birds that had established their own territories in the area, and resided in their territories. The latter were birds without, or outside, their own territories. The marked birds all had territories within the observation area, and were classified as territorial when they were in their own territories (each was about 2 m^2). However, when they were outside their own territories, they were classified as non-territorial. Because unmarked birds did not have territories in the area, they were always considered to be non-territorial. We recorded the behaviour of all of the gulls in the area on video for later analysis, on June 13, 14, and 16 for an hour each morning (0800–1200).

2) Video analysis

We examined the videos in the laboratory, using QuickTime player (Apple Computer Inc.) and jEdit (The jEdit Team) applications with additional scripts written by H. Hosoma (http://www.12kai.com/scr/).

First, we sought scenes in which territorial or non-territorial gulls gave long-call displays. Then, replaying the scenes, we observed birds within two metres of the displaying bird and recorded their behaviour before and after the long-call. Several birds were usually present within this two-metre area (including the partner, neighbouring territorial birds, and non-territorial birds), and we recorded their behaviour within five seconds before and after the displaying bird started its long-call. When two or more birds were present in the same direction with respect to the displaying bird, we only recorded the behaviour of the nearest bird.

We chose five of the eight marked pairs as focal pairs (10 birds), and measured the time when each individual was observed in its own territory, when each bird was alone or with its partner, and the frequency of long-call displays. These data were all collected from a total of three hours of video recorded on June 13, 14, and 16. The same material was also used to record each individual's behaviour immediately before or after its partner's long-call displays.

To investigate the responses of territorial birds to the long-calls of neighbouring territorial birds, we analyzed one hour of video recorded on June 13. Using the videos, we observed the behaviours of the neighbouring territorial birds surrounding the five focal pairs.

To investigate the responses of non-territorial birds to the long-calls performed by territorial birds, we analyzed one hour of video recorded on June 13. Using the videos, we observed the behaviours of the non-territorial birds surrounding the five focal pairs.

To observe the response of territorial birds to the long-calls of non-territorial birds, we analyzed two hours of video recorded on June 13 and 14. Using the videos, we first sought the long-calls performed by non-territorial birds, then observed the behaviour of the territorial birds surrounding the non-territorial birds.

Some videos we recorded for this analysis are

available on the internet at the web site: 'Video Archives of Animal Behaviour' (http://www.momo-p.com).

3) Definitions of behaviours and responses

The definitions of the observed behaviours are as follows. *Staying*: A gull remains standing in place or sitting on the nest without giving a long-call or choking display. *Attacking with the bill*: A gull pecks at other gulls with its bill or holds or pulls the wing or tail of another gull with its bill. *Intentional attack behaviour with the bill*: A gull directs its bill (usually open) at another gull and pushes it forward quickly. *Rushing*: A gull moves toward another gull rapidly, usually with its wings raised and spread and its bill open. *Approaching*: A gull moves toward another gull, but not rapidly. *Going away*: A gull moves away from another gull by walking, running, or flying. *Long-call display*: A gull jerks its head down deeply, giving one muffled call. Then, it throws up its head, giving a series of loud calls (Yabuta & Kawakami 2009). *Choking*: A gull squats, bends forward, and points its bill down. In this position, it repeatedly makes a rapid downward movement of its head as if choking or regurgitating.

Based on our observations of these eight behaviours, we classified responses to long-calls into the following six categories.

Stay response: If a bird stayed in place for five seconds after the displaying bird started its long-call, then the bird's response was classified as 'Stay'. However, if the bird approached the displaying bird before the long-call then stopped to stay after the call, this response was regarded as 'Avoid' (see below).

Avoid response: A bird's response was classified as 'Avoid' if it started to go away or stopped approaching after the long-call.

Approach response: A response was classified as 'Approach' if a bird started or kept approaching the displaying bird after the long-call.

Attack response: If a bird began 'attack with the bill', 'intentional attack with the bill', or 'rush' immediately after the long-call, then its response was designated as 'Attack'.

Long-call response: If a bird responded to a long-call display with its own long-call, then its response was classified as 'Long-call'.

Choking response: The response of a bird was designated as 'Choking' if it began choking after the long-call. However, even when a bird began choking before the displayer's long-call, if it kept choking for a long time (more than approximately two seconds) after the displayer started the long-call, then we considered that the bird had decided to continue choking and recorded choking as the response. However, if the time was short (less than two seconds), then we considered its subsequent behaviour as the response. Choking durations vary greatly (whereas long-call durations are fixed), implying that a choking bird decides when to stop. We consider that a bird decides to continue choking in response to a long-call, if the choking bird continued for a long time after the long-call.

In certain cases, the behaviours of birds we observed were clearly not responses to the displaying birds. For example, they sometimes flew away when rushed by a third bird (not the displaying bird). At other times, they attacked a third bird that approached too closely. We excluded such cases from our analyses.

3) Statistical analysis

To test whether the frequencies of responses differed depending on the context, we used Fisher's exact probability test for 2 by 4 contingency tables. Significant levels were set at $P=0.0083$ following Bonferroni correction (0.05/6).

RESULTS

1) Frequencies of long-call occurrence

During three hours of observation, each marked individual was observed in its own territory for an average of 1.7 hr (SD: 0.7, N=10). A total of 224 long-calls was recorded, at an average frequency of 12.7/h for each bird (SD: 3.7, N=10). The average time that each bird spent in its territory together with its partner was 20.2 min out of the three-hour observation period (SD: 21.1, N=10). The average duration when it was alone was 83.4 min (SD: 35.2, N=10). One of the five focal pairs was not observed together in its territory during the three-hour observation period. The remaining four pairs were observed together at least once. The average frequency of long-calls performed when each bird was in its territory with its partner was 38.0/h (SD: 23.6, N=8), whereas the average frequency of long-calls during the time when it was alone was 9.8/h (SD: 4.6, N=8). The former frequency was always greater than the latter for all eight birds, indicating that birds performed long-calls more frequently when with their partners than without them.

2) Responses to long-calls performed by territorial birds

During one hour of observation four female and three male neighbouring territorial birds (that is territory holders in adjacent territories) of five focal pairs were observed. In total, these seven birds performed, 85 long-calls. Females averaged 9.8 (SD: 6.1, N=4) and males 15.0 (SD: 2.1, N=3). When one of the seven neighbouring territorial birds gave its long-call display, 1–5 other territorial birds were in adjacent territories. We observed 206 responses of territorial birds to the display of neighbouring territorial birds. Most responded by Staying (78%). Some responded by Avoiding (8%) and others by giving Long-calls (7%). No Attack responses were observed.

When one of the seven territorial birds gave its long call display, 0–3 non-territorial birds were in the surrounding area of the displaying bird. We observed 59 responses from such non-territorial birds. Most Stayed (51%), or Avoided (32%), although some Approached (14%). No Attack responses were observed.

3) Responses to the long-calls performed by non-territorial birds

During two hours of observation, 22 long-calls by non-territorial birds were observed. When one non-territorial bird gave a long call display, 2–6 territorial birds were in the surrounding area. We observed a total of 77 responses from territorial birds. Most responded by Staying (74%). Some responded by Attacking (9%), or by giving Long-calls (8%). All of the displaying birds were unmarked, therefore they were not neighbours of the responding birds.

4) Responses to long-calls performed by partners

During three hours of observation, eight birds (four pairs) were observed together with their partners in their territories, and performed a total of 74 long-calls. We recorded the partners' responses of to those calls. Most responded by Staying (45%), or giving a Long-call (31%), while some Approached (12%). One Attack was observed. In this case, one member of the pair performed a long-call, to which its partner responded with its own long-call; the first bird then attacked the latter immediately after its long-call.

5) Differences in responses among contexts

The frequencies of Avoidance responses differed depending on the context (Fig. 1; $P<0.00001$, Fisher's exact probability test). Avoidance was the most frequently observed response when non-territorial birds responded to the long-calls of territorial birds.

The frequencies of Attack differed depending on the context (Fig. 1; $P<0.0001$, Fisher's exact probability test). Attacks were most frequently observed when territorial birds responded to the long-calls of

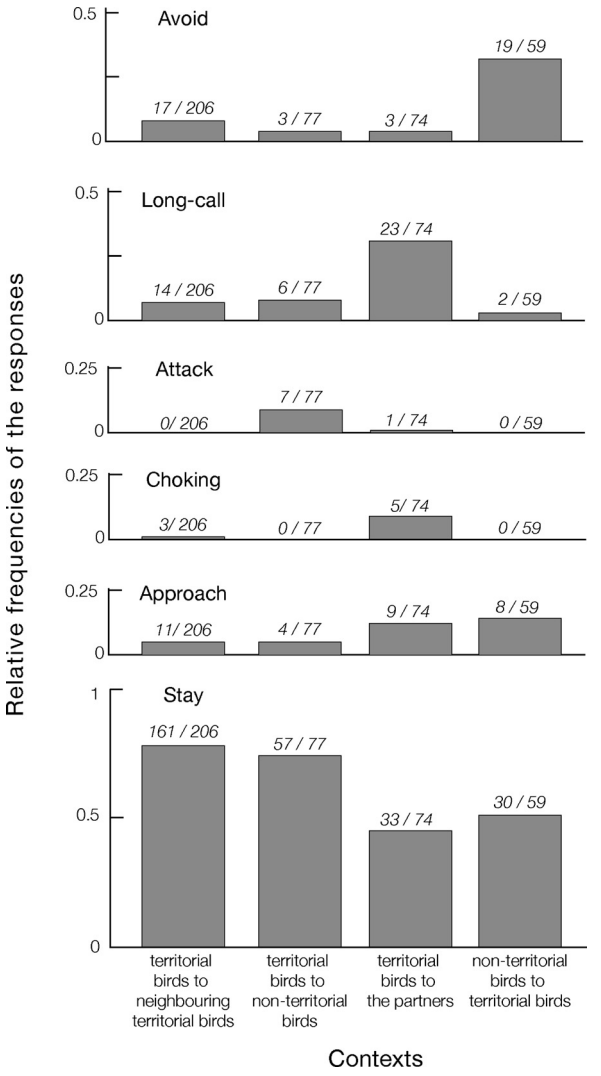

Fig. 1. Relative frequencies of each response are shown for four contexts. Left-most bars show the responses of territorial birds to the long-call displays of neighbouring territorial birds. Second left bars show the responses of territorial birds to the long-call displays of non-territorial birds. Second right bars show the responses of territorial birds to the long-call displays of the partners. Right-most bars show the responses of non-territorial birds to the long-call displays of territorial birds. Numbers above bars show occurrences of the response (numerators) and the total number of all responses (denominator) in the context.

non-territorial birds.

The frequencies of Long-calls, and of Staying, also differed depending on the context (Fig. 1; $P<0.00001$, Fisher's exact probability test). The Long-call response was observed most frequently when territorial birds responded to the long-calls of their partners. To long-calls of neighbouring territorial birds and non-territorial birds, a territorial bird showed Stay responses more frequently than the other two contexts.

The frequencies of Choking responses did not differ significantly among contexts (Fig. 1; $P=0.017$, Fisher's exact probability test). Note that the significant levels were set to $P=0.0083$ following Bonferroni correction (0.05/6). Similarly, the frequencies of Approach response did not differ among contexts (Fig. 1; $P=0.067$, Fisher's exact probability test).

DISCUSSION

The responses of Black-tailed Gulls to the long-calls of other individuals vary depending on the context. When territorial birds performed long-call displays, non-territorial birds often avoided them, whereas when non-territorial birds displayed, territorial birds often attacked them. Territorial birds often responded to the long-calls of their partners with the same long-calls. What mechanism causes this range of responses?

The results of the present study are explained well by the motivational conflict hypothesis, if the following details are assumed: Long-calls activate both the aggression and escape systems of other gulls, but the extent to which each system is activated depends on the context. The aggression system is likely to be activated when the bird is in its own territory. The activated level of escape system depends on the risk of a bird being attacked by another. In a colony, territorial birds frequently attack each other during squabbles over territory.

In cases where the displaying bird is territorial and the responding bird is non-territorial, the escape system of the responding bird is likely to be activated to a high level. Territorial birds represent potential danger to non-territorial birds, because they tend to attack. The aggression system of the responding bird, however, is not so activated because it is non-territorial bird (i.e. it is not in its own territory). Consequently, its escape system is likely to be activated to a higher level than its aggression system. According to the motivational conflict hypothesis, this causes the Avoidance response.

In cases when the displaying bird is non-territorial, and the responding bird is in own territory, the aggression system of the responding bird is likely to be activated to high level because it is in its own territory, while its escape system is not so activated because the displaying bird is non-territorial. Consequently, the aggression system is likely to be activated to a higher level than the escape system, engendering the Attack response (Fig. 1).

In cases when both the displaying and the responding birds are members of the same pair, each individual is territorial, and the aggression system is likely to be activated. Furthermore, the escape system is activated because the partner is another owner of the territory and therefore tends to attack other birds, even its partner. Attacks between mates are often observed in the field (Yabuta & Kawakami unpublished data). Consequently, both systems for aggression and escape are likely to be activated to a high level, engendering the Long-call response (Fig. 1).

When a displaying bird is a territory holder and the responding bird is a neighbouring territory holder, then both are territorial. In such cases, as in cases between mates, it is expected that long-call displays will be frequent. However, in this study, the frequency of Long-call responses was not particularly high (Fig. 1). Furthermore, the Avoidance response was also low, and no Attack responses were observed (Fig. 1). The reason for this may have been that observations were made during the post-hatching season, by which time territorial boundaries have already been clearly determined, and the probability of encroachment on a territorial bird's boundaries by neighbours is low. In addition, the probability of being attacked by a neighbour is low. Therefore, during this period, neither the aggression nor the escape system of a territorial bird is unlikely to be activated by the long-call of a neighbour.

Differences in the sound structure of long-calls may provide responding birds with important information and so may affect their reactions (Veen 1985). On the one hand, the sound structure of the long call may indicate to the responding bird the identity of the displaying bird and whether its aggressive motivation is high or low. Such information would help the responding bird assess the risk of being attacked by the displaying bird. On the other hand, the degree to which the aggression system is activated depends on the need or the subjective value of the territory for the displaying bird. In general, how animals respond to a

stimulus depends not only on the nature of the stimulus, but also on their internal state (Baerends et al. 1955). Variety in the responses to long-calls would also result from both the information content of the long-calls and the different tendencies to react of the responding birds.

Avian vocal displays elicit different responses from conspecifics in different contexts and, therefore, serve different functions (Mennill & Vehrencamp 2008). Are the responses to a certain display in different contexts controlled by different causal mechanisms? Our results show that Black-tailed Gulls often respond to their partners' long-calls with the same displays and that such a long-call response was observed also in other contexts (Fig.1). If the responses in different contexts are controlled by different causal mechanisms, we have to assume that more than two different causal mechanisms cause long-call displays. However, according to the motivational conflict hypothesis, we can explain the results more simply: long-call displays are always caused by a single causal mechanism. Furthermore, the motivational conflict hypothesis can also explain how responses other than long-call displays, such as avoidance and attack, occur. Therefore, we suggest that in every context, conflicting aggressive and escape motivations control responses to long-call displays by conspecifics. However, we do not rule out the possibility that when birds respond to their partner's long-call display, sexual motivation plays some role besides aggressive and escape motivations.

ACKNOWLEDGMENTS

We would like to thank the rangers protecting the gull colony on Kabu-shima for their help in the field.

REFERENCES

Baerends GP (1975) An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In: Baerends G Beer C & Manning A (eds) *Function and evolution of behaviour*. pp 187–227. Clarendon Press, Oxford.

Baerends GP, Brouwer R & Waterblk HT (1955) Ethological studies on *Lebustes reticulates* (Peters) I. An analysis of the male courtship pattern. Behaviour 8: 249–334.

Blurton-Jones NG (1968) Observations and Experiments on Causation of threat displays of the great tit (*Parus major*). Anim Behav Monogr 1: 75–158.

Dawkins R & Krebs JR (1978) Animal signals: information or manipulation? In: Krebs JR & Davies NB (eds) *Behavioural Ecology*. pp 282–399. Blackwell, Oxford.

Danchin (1991) Social Displays of the Kittiwake *Rissa tridactyla*. Bird Behaviour 9: 69–78.

Enquist M Plane E & Roed J (1985) Aggressive communication in Fulmars (*Fulmarus glacialis*) competing for food. Anim Behav 33: 1007–1020.

Hinde A (1970) *Animal Behaviour: a synthesis of ethology and comparative psychology. 2nd ed*. McGraw-Hill, New York.

Narita A (1997) The significance of Oblique-cum-Long-Call directed at other individuals of the Black-tailed Gull *Larus crassirostris*. J Nat Hist Aomori. (2): 16–18 (in Japanese).

Narita A (1998) The behavior chain of Oblique-cum-Long-Call of the Black-tailed Gull *Larus crassitostris* except that of directed at other individuals. J Nat Hist Aomori. (3): 1–3 (in Japanese).

Narita K & Narita A (2004) *Umineko-Kansatuki*. Kimura-shoten, Hachinohe (in Japanese).

McFarland D (1993) *Animal Behaviour: Psychobiology, Ethology, and Evolution. 2nd ed*. Longman, Essex.

Tinbergen N (1959) Comparative studies of the behaviour of gulls (Laridae): a progress report. Behaviour 15: 1–70.

Mennill DJ & Vehrencamp SL (2008) Context-dependent functions of avian duets revealed through microphone array recordings and multi-speaker playback. Curr Biol 18: 1314–1319.

Veen J (1985) On the functional significance of long call components in the little gull. Neth J Zoo 35: 63–86.

Veen J (1987) Ambivalence in the structure of display vocalizations of gulls and terns: new evidence in favour of Tinbergen's conflict hypothesis? Behaviour 100: 33–49.

Yabuta S (2002) Uncertainty in partner recognition and the tail-up display in a monogamous butterfly fish. Anim Behav 63: 165–173.

Yabuta S (2008) Evolution of cross-contextual displays: the role of risk of inappropriate attacks to non-opponents, such as partners. Anim Behav 76: 865–870.

Yabuta S & Kawakami H (2009) Long-call display of black-tailed gull. Movie Archives of Animal Behavior Data No.: momo090809lc01b (http://www.momo-p.com/showdetail-e.php?movieid=momo090809lc01b).