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Anti-Predator Responses of Black-Tailed Gull (*Larus crassirostris*) Flocks to Alarm Calls during the Post-Breeding Season

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ABSTRACT: Black-tailed gulls (*Larus crassirostris*) produce alarm calls apparently related to their anti-predator behaviors, but the hypothesis that the calls are actually used as functionally referential alarm signals has not yet been tested. In this study, we performed a series of experiments using visual (a stuffed goshawk: *Accipiter gentilis*) and acoustic (alarm calls and a control vocalization) stimuli at 15 sites in Sinjindo-ri and Dowhang-ri, Taean-gun, Chungnam province to examine anti-predator responses of the gulls to alarm calls in playback trials. We found that the gulls' visual recognition of a perched hawk model in the absence of alarm vocalizations was weak or absent because the model was noticed in only two out of 16 trials. The gulls' responses to playbacks of the alarm call only and the alarm call with a visual stimulus differed from responses to the control vocalization in latency to approach, time mobbing, and the percentage of gulls responding, while the responses to alarm call only differed from alarm call with a visual stimulus in latency to first fly, latency to call, and time mobbing. The results of this study suggest that alarm calls of black-tailed gulls are used to elicit appropriate anti-predator behaviors that are intensified when a predator is detected visually.

Key words: Alarm call, Avian communication, Black-tailed Gull, *Larus crassirostris*, Mobbing

INTRODUCTION

During the evolution of avian vocal communication, most bird species have developed vocal repertoires closely adapted to their social and physical environments (Sordahl 1979, Johns and Falls 1989, Trainer and McDonald 1993). Many studies have examined the acoustic structure and vocal functions of bird calls (e.g. Oring 1968, Ficken et al. 1978, Anderson 1978, Maier 1982, Riska 1986, Anjos and Vielliard 1993, Byers 1996), yet for most bird species, the functions of common vocalizations are poorly understood. Animal signals may provide information about the internal state of the signaler, or may include information about external events (referential communication). Two criteria have been proposed for the recognition of acoustic structures as referential acts of communication (Marler et al. 1992, Evans 1997). First, a species must produce stimulus-specific signals, so that vocal repertoire of the species can be classified into distinct call types and the meaning of each call type can be inferred from the behavioral contexts of call use. For example, the presence of a fox near a nest should elicit the appropriate vocalization, a 'distraction call', produced while adults attempt to distract a predator away from a nest. Second, the species must appropriately distinguish the signals in the absence of other stimuli (context-independent perception) and respond to each signal differently and appropriately in playback experiments.

The black-tailed gull (*Larus crassirostris*) is a sea bird which is locally abundant in Korea, and breeds on islands. As black-tailed gulls nest colonially in ocean environments, their calls must overcome background noise, such as the sound of wind, ocean waves, and other bird calls, to effectively transmit signals across short and long distances. Gull vocalizations display several characteristics which may improve sound transmission in this type of environment, including: 1) low frequency, which may reduce the attenuation rate; 2) frequency-modulated tones, which may prevent calls from being distorted; 3) broad band sounds, which are easily detectable; and 4) amplitude modulation, which may reduce degradation (Morton 1975, Wiley and Richards 1982). Calls are often performed during aerial displays, which may also improve the efficiency of signal propagation. Park and Park (1997) described the vocalizations of adult black-tailed gulls, and identified eight different vocal signals grouped into three functional classes: contact calls (three call types), alarm calls (two call types), and aggressive calls (three call types). Calls were identified based on their acoustic structure and classified using the behavioral contexts of call use. The specificity of the contexts in which gull calls are produced suggests that some gull vocalizations may meet the first criterion for recognition as acts of referential communication. However, it is not yet clear whether black-tailed gull calls elicit appropriate behaviors independent of their context, which

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is required to demonstrate that the signals are functionally referential.

In this study, we examined the role of a single type of black-tailed gull alarm call to determine whether this call functions to warn other individuals of danger. Our experiments involved a black-tailed gull alarm call identified by Park and Park as call type 1 (1997). Call type 1 is composed of one to four brief sounds emitted in rapid succession and is usually produced when a predator is approaching a nest or enters a colony. The call stimulates nearby gulls to gather in a flock to search for and mob potential predators (Rho 1992). The resulting mobbing behavior is associated with the production of an additional vocalization, a mobbing call, which resembles the mew call described by Park and Park (1997). We will describe the structure and function of the mobbing call elsewhere.

If the call functions to warn others of danger, then alarmed individuals should respond appropriately, either by immediately escaping (Tinbergen 1960), or aggressively mobbing potential predators. We will refer to vocalizations resulting in flight as "flee alarms", and vocalizations resulting in mobbing of predators as "mobbing alarms". In this study, we examined the following questions: 1) Do alarm calls of type 1 result in appropriate anti-predator responses more often than the control vocalization (a mew calls)? 2) Do gulls display more intensive anti-predator responses in the presence of a visible predator (a stuffed goshawk: *Accipiter gentilis*) than in the absence of a visible predator? We predicted that if alarm calls of type 1 function as a referential act of communication indicating the presence of a predator, then the subjects will produce appropriate behavioral anti-predator responses to the playbacks of alarm calls in the absence of any additional cues of predator presence. We further predicted that the call will function as a flee alarm, because we performed playback experiments during the post-breeding season, during which mobbing behavior should offer little benefit. Finally, we predicted that responses of the subjects to alarm calls in the presence of a visual stimulus (a stuffed hawk) will be stronger due to the presence of mutually reinforcing visual and acoustic stimuli.

MATERIALS AND METHODS

We studied populations of black-tailed gulls resident in the vicinity of Sinjindo-ri and Dowhang-ri, Taean-gun, Chungnam province (Fig. 1). The playback experiments were conducted during the post-breeding season, when immature and mature gulls forage and rest in groups of tens of individuals. Gulls of other species (e.g. *Larus argentatus*) are also included in these groups, which therefore comprise mixed-species flocks.

To investigate the role of alarm calls, playback experiments were conducted to test whether the gull flocks discriminate between the type 1 alarm call and a control vocalization, the mew call. We used the mew call as an experimental control because this call was not produced in the presence of predators, but rather seemed to be used primarily as a contact call by parents and chicks or pair mates. In an additional set of experiments, we introduced a visual stimulus (a stuffed hawk) to the playback trials to determine whether gull flocks respond to type 1 alarm calls by locating and mobbing visible predators.

Fig. 1. Map of Sinjindo-ri and Dowhang-ri (below), Taean-gun, Chungnam province (above). Dots indicate the locations of playback experiments in this study. Grey areas are included in Taean-gun.

Playback experiments were conducted using four different treatments: 1) a stuffed-perched hawk was presented to gull flocks without any acoustic information; 2) the stuffed hawk was presented with playbacks of alarm calls; 3) playbacks of alarm calls were presented without the stuffed hawk; 4) playbacks of mew calls (the control vocalization) were presented. The four treatments were presented in random order with 10 min gap between trials if there were no responses. We established 15 playback sites in areas that gulls frequently gathered together, and we then randomly chose sites for 29 playback trials from among the established sites. Playback trials were conducted on four days from 21 October to 10 November 2006.

We recorded alarm calls (call type 1) produced in response to the presentation of a stuffed hawk, and spontaneously produced mew calls from captive males using a Marantz PMD222 tape recorder and condenser microphone (type MKH 816 P48, AKG c1000s). Playback tapes for the experiments were then prepared using Raven 1.2 (Cornell Laboratory of Ornithology 2004) with sampling rate 44.1 kHz and Cool Edit Pro. 1.5 (Adobe® Audition™ software). Ninety-second playback tapes containing either 28 alarm calls or 16 mew calls were produced. The alarm calls used in the recording consisted of three identifiable parts with a 2.58 sec inter-call interval and a 0.435 sec call duration, while the mew calls are identical with 5 sec inter-call interval and 0.41 sec call duration (Figs. 2, 3). Inter-call intervals for the two playback recordings were close to the natural calling rate from the sampled individuals.

We conducted the experiments on mixed groups of gulls between 0700 h and 1800 h on days when weather conditions were good (i.e. days without heavy wind or rain). We used a Sony portable minidisc recorder (MZ-R700) for the callbacks, and placed the speaker (JBL-Pro III) in various places at a distance of 80.4 m ± 29.0 (range: 32～137, n=46) from the resting gulls. For the experiments involving a visual stimulus, we placed a stuffed hawk 30 cm above the ground on a box just next to the speaker. The average intensity of the call playback was 80 dB (Larson-Davis Lab. Model 800B) at 20 m from the speaker. Before conducting each experiment, we monitored the sites to count the number of mature and immature flock members (regardless of the species). We started the experiments after confirming that the absence of any natural disturbance, but if a natural disturbance occurred during the experiment we stopped and moved to another site. We videotaped the whole playback session with a Sony 8 mm Hi-Fi camcorder for further detailed analyses of the response patterns of the flock members.

To examine differences in behaviors of the gull flocks during and after the playback experiments, we measured the following: 1) latency to first flight (sec; time from the start of the experiment to the first response); 2) latency to call (sec; time from the start of the experiment to the first mobbing call); 3) latency to approach (sec; time from first flight until the first gull approached the speaker); 4) time mobbing (sec; duration of time gulls spent flying over short distances, turning sharply back and forth between the speaker and the resting site, starting from the first gull's arrival at the speaker); 5) number of mobbing calls given in five minutes; 6) number of gulls responding (obtained by subtracting the number of birds remaining after playbacks from the initial number of flock members).

Data were analyzed using SPSS statistical software (v.11.5; SPSS 2002). We tested the data for significant deviations from normality prior to the use of parametric statistical tests (One-sample Kolmogorov-Smirnov test, $P<0.05$). If the data met the assumption of normality, then the anti-predator responses of flock members in the experimental treatments were compared using one-way ANOVA and multiple post-hoc comparisons (Tukey test). As the response variables are likely to be correlated, we then used principal component analysis (PCA) to summarize most of the variance in the original variables and to create composite scores for each treatment.

The Varimax method was used to rotate the principle component

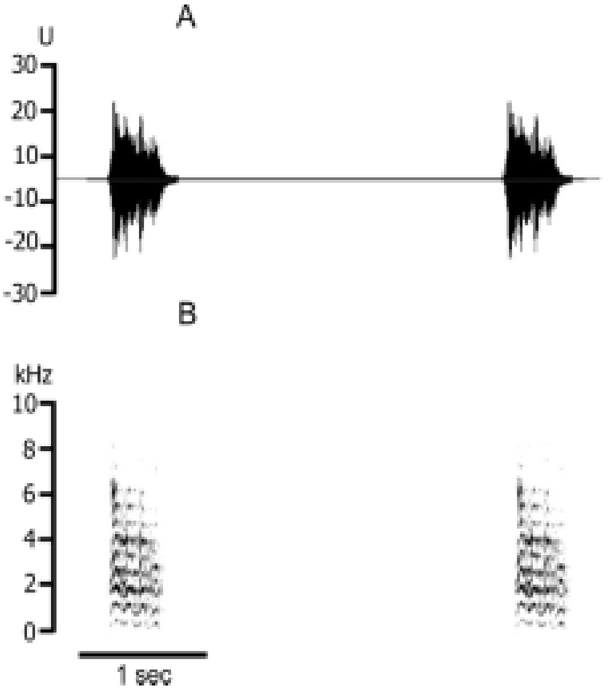

Fig. 2. Parts of black-tailed gull alarm calls used for the playback experiments. Alarm calls consist of a series of staccato, low-pitched brief calls repeated at 2.58 sec intervals. A - waveform; B - sonogram.

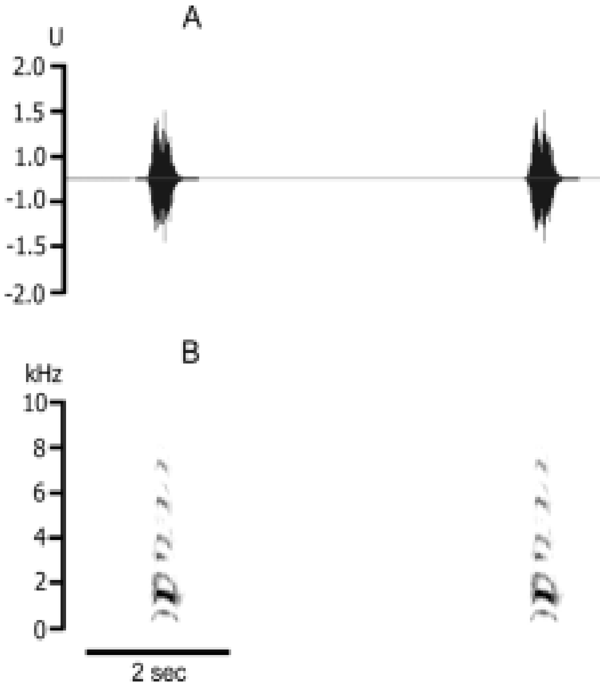

Fig. 3. Parts of black-tailed gull mew calls used as the control for the playback experiments. Mew calls consist of a series of sound bursts repeated at 5 sec intervals. A - waveform; B - sonogram.

(PC) factor loadings and then the PC scores for the first two principle components were compared among three experimental groups. Numerical data are presented as mean ± SD.

RESULTS

The stuffed-perched hawk presented without an auditory stimulus was detected only twice in 16 trials. In these two cases, when one of the adult flock members detected the presence of the hawk and emitted mobbing calls, all other flock members flew in irregular patterns, creating a swirling mass, and then left the area immediately. In two additional trials conducted at a single fairly windy site, the presentation of the alarm call, or the alarm call with the stuffed hawk failed to evoke mobbing behaviors. As we could not be certain that the gulls actually perceived the playbacks against the background noise from the wind, we excluded these data from further analysis for comparisons among treatments.

The responses of the gulls to the three treatments significantly differed in all six response variables: latency to first fly ($F_{2,26}$=4.584, p=0.02); latency to call ($F_{2,26}$=4.826, p=0.017) with a significant difference between the response to the playback with a model predator and the responses to the other two treatments; latency to approach ($F_{2,26}$=21.118, p<0.001); time spent mobbing ($F_{2,26}$=15.292, p<0.001); number of mobbing calls ($F_{2,26}$=4.774, p=0.017); and number of gulls responding ($F_{2,26}$=5.409, p=0.011) (Fig. 4). Post hoc pair-wise comparisons between treatments revealed that the responses of gulls significantly differed (Tukey test, p<0.05): 1) between to the control playback on the one hand and to playbacks of the alarm call with or without the model predator on the other in two variables (latency to approach, Fig. 4E; gulls responding, Fig. 4F), 2) between the control playback and the alarm call playback on the one hand, and the playback of the alarm call with the model

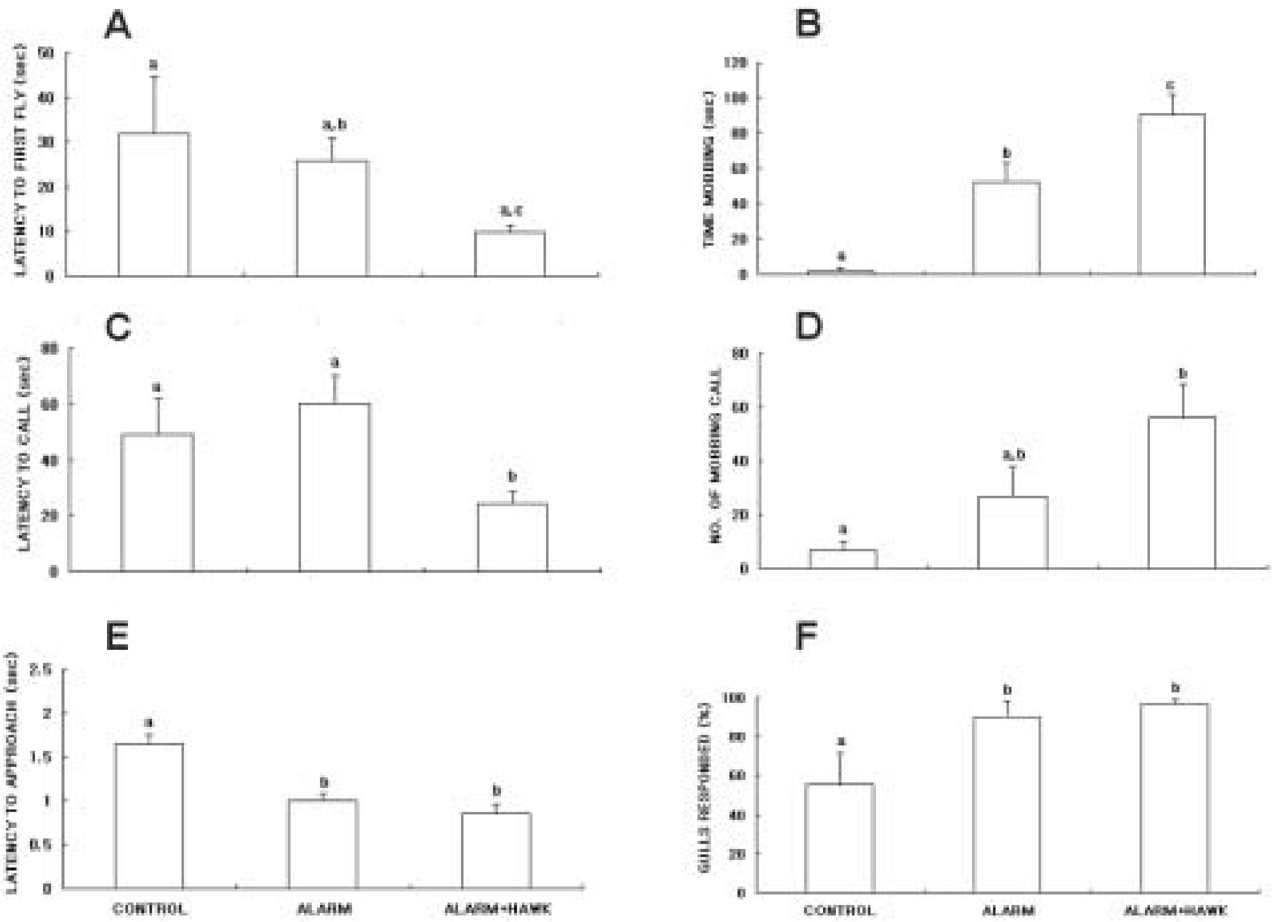

Fig. 4. Behavioral responses of gull flocks during the post-breeding period to mew calls (control), alarm calls only, and alarm calls with a stuffed hawk. Bar represent mean ± SE. Significant differences among the three experimental treatments were detected for all six response variables; the use of the same superscript letter indicates means that were not significantly different in post-hoc pair-wise comparisons (Tukey test, p>0.05).

predator on the other hand in the two variables (latency to first fly, Fig. 4A; Latency to call, Fig. 4C), 3) between the control playback and the playback of the alarm call with the model predator in one variable (number of mobbing call, Fig. 4D), and 4) in each set of pair-wise comparisons among the three experimental treatments in one variable (time mobbing, Fig. 4B).

Table 1. Loadings of the response variables on the two principal components

	Loadings	
Response variables	PC1	PC2
Latency to first fly (s)	0.903	−0.055
Latency to call (s)	0.882	−0.078
Latency to approach (s)	−0.214	−0.922
Time mobbing (s)	−0.443	0.697
No. of mobbing calls	−0.572	0.487
Gulls responded (%)	−0.503	0.600
Variance explained	40.26%	32.37%
Eigenvalue	2.416	1.942

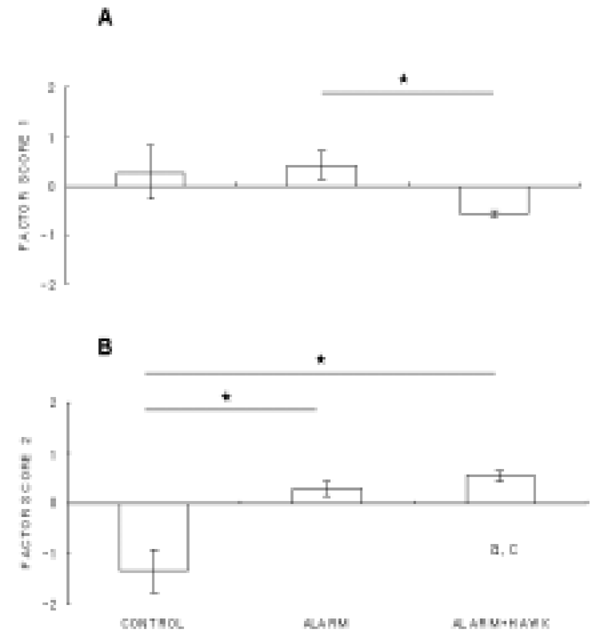

Fig. 5. Mean (± SE) values of principal components for behavioral responses of gulls to playbacks of mew calls (control vocalization), alarm calls (without a visual stimulus), and alarm calls with a stuffed hawk. The scores of two components significantly differed among the three playbacks; Asterisks indicate significantly different responses to playback calls in post-hoc pairwise comparisons (Tukey test $p<0.05$). A - Principal component 1; B - Principal component 2.

Two principal components (PCs) with eigenvalues were extracted based on the six behavioral variables (Table 1). PC1 explained 40.26% of total variance with high positive loadings for latency to first fly and latency to call variables, and scores significantly differed among the three treatments ($F_{2,26}=3.523$, $p=0.017$). Post-hoc comparisons revealed a significant pair-wise difference between scores for the alarm call playbacks and alarm call playbacks with visual stimulus (Tukey test, $p<0.05$; Fig. 5A). PC2 explained 32.37 % of total variance with a high negative loading for latency to approach and moderate positive loadings for time spent mobbing and number of gulls responding, and scores significantly differed among the three treatments ($F_{2,26}=19.246$, $p<0.001$). Post-hoc comparisons detected significant differences between a) the control and alarm call playbacks, and b) the control playback and the alarm call playback with visual stimulus (Tukey test, $p<0.05$; Fig. 5B).

DISCUSSION

Our prediction that an acoustically distinctive alarm call produced by black-tailed gulls would be sufficient to elicit anti-predator behaviors in the absence of the predator was supported by our playback experiments. When compared with the control playbacks, the response of gulls to playbacks of alarm calls was more intense in the following ways: more gulls responded, gulls approached the source of acoustic information more rapidly, and gulls mobbed the speaker longer. In addition, in comparisons of alarm call playbacks with and without a visual stimulus (a stuffed hawk), the gulls produced mobbing calls more rapidly and mobbed the speaker longer in the presence of a detectable predator. The present results indicate that mixed-species flocks consisting of black-tailed gulls and a few gulls of other species respond to the alarm call with appropriate anti-predator responses, and that these behaviors are intensified in the presence of a predator.

The dramatic responses to the alarm calls observed in these experiments are rather surprising for three reasons. First, as the call was primarily emitted when the predator was seen but did not pose an immediate threat. We had expected the gulls to be attentive to the predator, or to escape the resting area in the presence of a stuffed hawk, but not to mob the predator, which would confirm that this alarm call is used as a flee alarm call (Tinbergen 1960, Gilchrist 2001). However, in our experiments, the call typically induced mobbing behaviors by the gulls. Second, behavioral observations suggest that gulls mainly produce alarm calls in the nesting area during the breeding season, and that the intensity of calls varies with the stage of parental care. For example, the intensity of alarm calls peaked at hatching of nestlings in breeding colonies of common gulls (*Larus canus:* Budrys and Gegelevičius 2002) and black- headed gulls (*Larus ridibundus:* Malickiene and Budrys 2002). At this time, gull chicks are highly vulnerable due to their inability to escape predators on their own (Andersson et al. 1980) and their vulnerability to harsh weather conditions, such as cold or heat (Dale et al. 1996). As this study was performed after the breeding season, we expected the behavioral responses to alarm call to be of low intensity, and to decline with the increasing ability of offspring to escape from predators on their own. However, in playback experiments, over 90% of the flock members immediately took flight following the responses of one or a few flock members to the alarm call and the responding gulls repeatedly uttered loud and easily localizable mobbing calls, apparently to attract neighbors to assist in monitoring or repelling the potential predator (Curio 1978, Bradbury and Vehrencamp 1998). Furthermore, contrary to our expectation that gulls would flee the playback area, the birds actually approached the source of acoustic information (and the visual stimulus, when it was presented) by flying low and circling at some distance from the source. The active mobbing behaviors of the post- breeding birds (mature and immature gulls) suggest that they are responding to potential predation risk to themselves (Andersson et al. 1980), and not just to hatchlings. Thus, the alarm call can be used to induce mobbing behaviors during the post-breeding season. Third, perched models of avian predators should be perceived as posing less risk than flying models, and therefore should be mobbed less intensively. Rho (1992) reported that black-tailed gulls respond to avian predators flying over the breeding colonies by mobbing them, but no information is available about responses to perched predators at breeding and post-breeding colonies. In our experiments, few gulls responded to the presentation of the stuffed hawk without acoustic cues at a mean distance of 80.4 m (± 29.0) from the resting area. Therefore, we can infer that the visual recognition of predation risk from a perched hawk at this distance is weak or absent for resting flocks. Furthermore, previous studies of passerines have reported no mobbing or less-intense mobbing in response to perched predator models rather than flying models (Bildstein 1982, Lind et al. 2005). Nevertheless, in this study, alarm calls coupled with a perched model hawk induced stronger anti-predator responses than did alarm calls alone.

Mobbing as an anti-predator behavior is widespread among colonial breeding birds, including black-tailed gulls. Previous studies have suggested that mobbing calls and behaviors may affect both predators and conspecifics; mobbing generally functions to announce the presence or approach of the predators to conspecifics while simultaneously annoying the predators and encouraging them to leave the mobbing site (Marler 1955, Curio 1978). In our study, the mobbing activities of the gulls were influenced by the presentation of a perched hawk model: the gulls responded with mobbing calls earlier and mobbed the speaker longer in the presence of the hawk model than they did in its absence. When the playbacks of alarm calls ended, the mobbing behavior almost immediately disappeared in the absence of the model hawk [time mobbing after the end of the playback (sec)=0.09±29.65 (n=11)] whereas the mobbing behavior persisted for approximately 20 seconds after the end of the playback in presence of the model hawk [time mobbing (sec)= 19.55±44.16 (n=11)]. This result suggests that mobbing behavior induced by the playback of the alarm call leads to search for potential predators during the playback, and that behavioral responses persist in the presence of either ongoing alarm calls or a detectable predator. Thus, the alarm call may be interpreted as an honest signal by the receivers.

The structure of the type 1 alarm call of black-tailed gulls is similar with that of alarm calls of several other gull species, (e.g. *Larus occidentalis:* Hand 1981; *Larus livens:* Hand 1981; *Larus hyperboreus:* Gilchrist 2001; *Larus delawarensis*: Ryder 1993), consisting of a series of staccato, low-pitched, and brief call repeated in rapid succession. The volume of black-tailed gull alarm calls seemed much lower than that of mobbing calls, although we did not directly measure call intensities. The lower intensity of alarm calls could be due to their primary use for short-distance communication among group members, whereas the higher intensity of mobbing calls may be necessary to attract more distant conspecifics and to repel potential predators. Another reason for the lower intensity of alarm call may be that alarm calls are mainly given by gulls on the ground whereas mobbing calls are mainly given in flight, which may improve sound transmission in open habitat.

In this study, about 50 % of mature and immature gulls responded to playbacks of mew calls (the control vocalization) and responses to the control and alarm call playbacks did not differ for the variables latency to call and latency to first fly. We do not know why the mew call elicited these responses, but believe that these responses may result from acoustic similarity between mew calls and mobbing calls. The mobbing call was only recently identified, and its relationship with alarm calls is still being clarified. Park and Park (1997) also pointed out that during aggressive encounters with intruders, the mew call may function to promote aggressive behaviors, which may explain the surprisingly strong reactions to this call in our experiments. Further research on the structural features and potential functions of black-tailed gull calls will clearly be required to better understand the roles of each type of call, and address the question of whether black-tailed gull alarm calls function as acts of referential communication.

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