

Offspring-defence behaviour towards a human intruder in three species of gulls: *Larus marinus*, *L. argentatus* and *L. canus*

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I studied the behaviour of three species of gulls (Great Black-backed, Herring and Common Gull) when I entered breeding colonies, or in the case of the Great Black-backed, the territories of solitary pairs. When rearing chicks, all three species react towards the intruder by circling above the intruder (passive mobbing), or swooping down on him (active mobbing). Direct attacks usually end before the gull touches the intruder, but some pairs attack fiercely, striking with their feet. Herring and Common Gulls also performed a “distraction display” involving low flight above the sea with (sometimes) trailing feet. The results suggest a change in behaviour between the incubation and the chick rearing period, during incubation many pairs seemingly ignore the intruder, or remain inconspicuous. Great Black-backs never landed on the water during disturbances. Great Black-back pairs seem to be attackers more often than pairs of the other two species. In colonies, Herring and Common Gull pairs attack at their territories, and only a fraction of all pairs are attackers. I found no indication of “communal defence”. I suggest that in large colonial species at least there is a benefit in returning synchronously, and that the gain from flocking for passive mobbers is that they can protect their offspring from neighbours by landing synchronously with the other colony members once the disturbance is over.

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Introduction

Flocking around a potential predator is typical behaviour in the breeding colonies of many *Larus* species. This flocking is usually called mobbing (see Conover 1987, Shields 1984), sometimes predator-attraction behaviour (Kruuk 1976), and as the birds also charge and attack the predator it may be defined as offspring-defence behaviour. Mobbing gull flocks often consist of birds that actively attack predators, and birds that do not attack predators (active vs. passive mobbers, Kruuk 1964, 1976, Shields 1984, Conover 1987).

Active mobbing probably serves mostly to repel predators. The function of passive mobbing, though widely discussed (Curio 1978), is still uncertain. It might be a kind of “distraction display” (Nice 1943), serving to confuse the predator (Curio 1978).

In several species of waders, a classic distraction display is “injury feigning” which serves to attract the predator’s attention in order to save the offspring

(Gochfeld 1984). Distraction displays have been reported very occasionally in the Black-headed Gull *L. ridibundus* (Kruuk 1964). They are more subtle than vigorous attacks, though conspicuous, and are uncommon among gulls, though well developed among the related skuas (*Stercorarius* spp., see Gochfeld 1984 for an excellent review).

I recorded offspring-defence behaviour in three species of gulls, the Great Black-backed Gull *Larus marinus*, the Herring Gull *L. argentatus* and the Common Gull *L. canus*. The purpose was to describe the behaviour and displays used, and to check whether there were any differences between the species. The two smaller species nest colonially in the archipelago of SW Finland, while the Great Black-backed Gull is primarily a solitary breeder (Bergman 1982). During a previous study on the Herring Gull (Kilpi 1987a), I observed some indications of pronounced individual variation in offspring defence behaviour. Quantification of such differences was another purpose of the present study.

Study area and methods

I observed gull behaviour off Hanko, SW Finland during the 1987 breeding season, primarily in one colony of Herring Gulls (38 pairs), two Common Gull (19 and 36 pairs) colonies, and on territories of 22 solitary Great Black-backed Gull pairs (with occasional visits to other colonies and sites). The area and the colonies have been described in other papers (Kilpi 1987a, 1987b). Human intrusion is one of the main factors affecting breeding success in gulls in this area (Kilpi 1987b), and persecution of gulls is a tradition in the study area.

I always approached the colonies and the breeding sites by boat, landed rapidly and immediately entered the main colony or territory, all of which are known to me from previous years. I then usually walked through the colony in a zig-zag fashion at fairly constant speed for 10 minutes and recorded gull behaviour. At Great Black-backed Gull sites I usually spent 5 minutes in the territory. In colonies, I often spent up to 30–45 minutes, but used only data from the first 10-minute period when recording mobbing behaviour and attack rates for to the whole group. I recorded the absolute number of attacks/minute during the zig-zag walk (attack frequency). The attack rate was obtained by scaling the attack frequency for flock size (attack frequency/ number of potential mobbers). In Figs. 2–3, the attack rate has been multiplied by a factor of 10 for convenience of presentation. I also recorded attack frequencies at individual territories within colonies during the chick rearing stage. I did this while handling (ringing) chicks (see Conover 1987), which usually makes the reactions of adults more vigorous.

I recorded vocalisations only for Great Black-backed Gulls.

Results

Behaviour in the territory and colony

Great Black-backed Gull. After being put up from the nest site, Great Black-backs either attacked or just circled in the air above the site, some at distances of over 200 m, silent and inconspicuous. A total of 38 separate visits (189 minutes) involving 22 pairs were made during early incubation until the chicks were large, and not a single bird settled on the water while I was at the site. While circling above the site, the birds remained silent, or uttered a deep, short *ga-ga*

with varying intensity, combined the *ga-ga* with a long *glao*, or uttered a constant mixture of *ga-ga* and *glao* calls, here interpreted qualitatively in increasing order of intensity. When silently attacking the intruder the gulls descended at an angle of about 45° or steeper to the ground, and then uttered rapid *ga-ga* calls after the attack had been delivered. The distance at which the stoop ended varied between individuals. Two individuals of different pairs did their best to strike me on the head, in the typical “charge” fashion with out-stretched legs as described for the Herring Gull by Tinbergen (1956). Only one of the birds of a pair attacked. The other bird remained circling around the nest site. On many occasions, their behaviour attracted neighbouring pairs and also Great Black-backs with sub-adult plumage and a few Herring Gulls. Thus, up to 10 individual Great Black-backs could circle above the site of a single pair. On 13 visits, territory owners were joined by strange Great Black-backs (34% out of 38 visits, maximum number of strangers 8) and three times also by Herring Gulls (max. 4). The strange Great Black-backs were attacked by the territory owners on 12 of the 13 visits (92%), and Herring Gulls were attacked once.

Herring Gull. Herring Gulls show the same responses to an intruding human as Great Black-backs (see also Tinbergen 1956). The most striking difference is that some of them ignore the intruder and gather on the sea surface (see also Kilpi 1987a, and below).

Some Herring Gulls attack an approaching boat. Herring Gulls also exhibit a distraction display (flying low above the sea with trailing feet, sometimes touching the surface, or flying slowly away from the colony 1–3 meters above the surface) described for Common Gulls (Gochfeld 1984, see also Vermeer & Devito 1986). The intensity of this display varies, the version with trailing feet seems rare, and I saw it performed on only one occasion by one bird. I observed distraction displays on three out of a total of 16 visits to the study colony. All these were during the chick stage and they were recorded for 1 (1% of all present), 2 (3%) and 10 (13%) birds. On the last occasion the first chicks had entered the water. The display was initiated only after I had re-entered my boat after the visit.

Common Gull. Common Gulls show the same display repertoire as Herring Gulls. The distraction display was rare. As in Herring Gulls, I observed it only after the chicks had hatched. It was performed on three occasions out of 8, and in only one study colony,

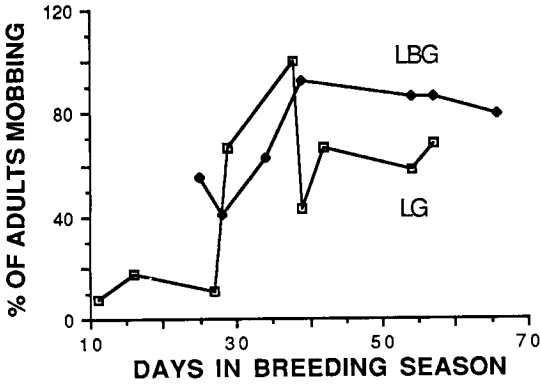


Fig. 1. Proportion of adult gulls present participating in active mobbing in the two Common Gull colonies (LG = Långgrund, LBG = Långbodagrynnna). Those not mobbing remain sitting on the sea surface. The arrow indicates the median date of hatching. The starting date is May 10.

once by one bird (3% of the birds in that colony), and twice by 2 birds (5% and 7%), all three times after the median hatching date. The lack of this display in the other colony was probably due to the successive loss of nearly all chicks shortly after hatching. The Common Gulls started the distraction display while I was still in the colony.

Defence displays in relation to breeding stage

Previously (Kilpi 1987a) I showed that Herring Gulls remain on the water during disturbances only during early breeding. I found a significant increasing trend in actively mobbing adults up to the median date of hatching. The present data suggest a similar trend for percentage mobbing, for the absolute number of attacks when I was walking through the colony and the attack rate scaled for flock size ($r_s=0.70$, $n=10$, $P<0.05$, $r_s=0.72$, $n=10$, $P<0.05$ and $r_s=0.75$, $n=10$, $P<0.05$ respectively). The trends were tested on records made prior to the date that chicks started escaping into the water. My records for Common Gulls suggest a similar increase in adults engaging in active mobbing (Fig. 1). The numbers of attacks and attack rates in the two Common Gull colonies are shown in Fig. 2. The material is small, but it shows an increase in the attack frequency as the season advances in one colony of Common Gulls (Spearman rank correlation, $r_s=1.0$, $P=0.01$, $n=6$), and a higher attack rate with advancing season ($r_s=0.96$, $P<0.05$,

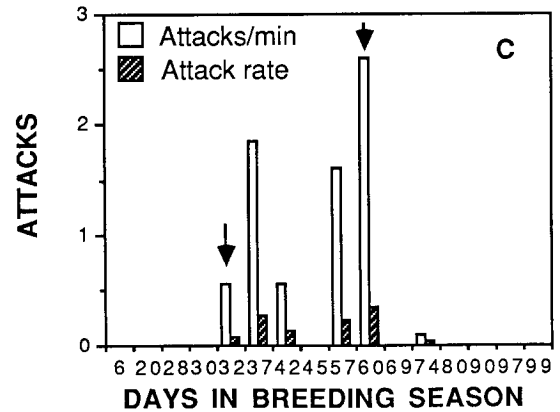
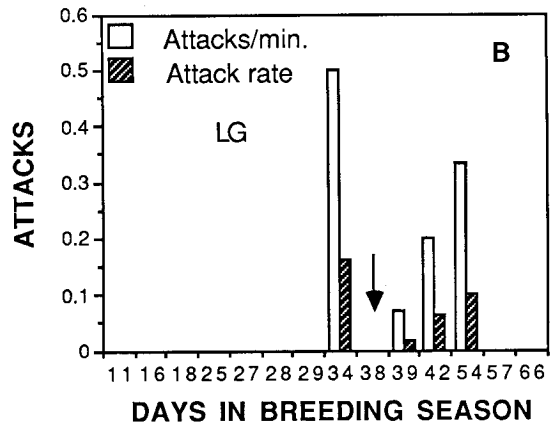
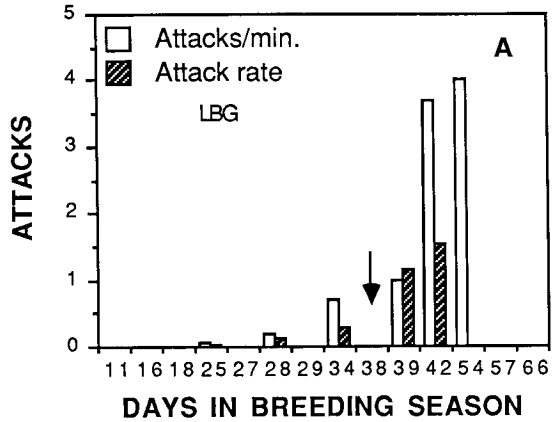


Fig. 2. Attacks/minute and attack rate in the two Common Gull colonies (LBG and LG, graph a and b) and the Herring Gull colony (c). The arrows indicate: in (a and b) the median date of hatching, in (c) the median date of hatching, and the date when the first chicks escaped into the water when disturbed. In the other Common Gull colony (LG) almost all chicks were lost before fledging. The starting date is May 6.

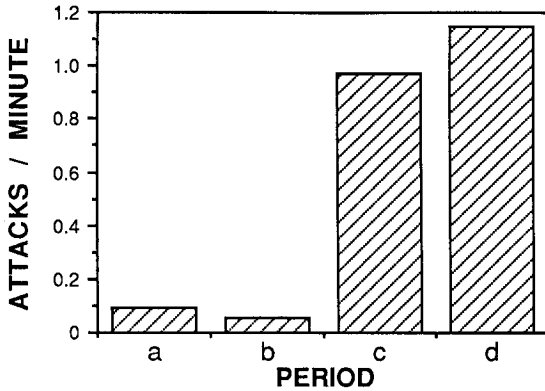


Fig. 3. Attacks made by Great Black-backed Gulls during early (a) and late (b) incubation, and when rearing small (c) and large (d) chicks. The observations were made once per pair and period involving 11, 11, 8 and 8 pairs, respectively. Some pairs were the same in the different periods.

n=6). On the last visit the first chicks had fledged, many escaped into the sea and attacking had ceased. Attacks end once the chicks flee into the water during disturbance (see also Kilpi 1987a).

Fig. 3 shows the response of Great Black-backed pairs during incubation and chick rearing. I then pooled the data for the incubation period and the chick-rearing period and examined circling distances and vocal responses. I used two categories for vocal response: silent pairs or calling pairs, and for circling distances: closer than 50 m or further off than 100 m. The reactions to me seemed to be more intense during chick-rearing than during incubation as concerns both vocal responses and circling distances. During incubation, 94% of the pairs (n=17) circled at distances >100 m, while only 14% (n=7) did so during chick rearing (Fisher's exact probability test, P=0.00). Correspondingly, 70% of the pairs (n=17) remained silent during incubation, while only 14% (n=7) did so once the chicks had hatched (Fisher's exact probability test, P=0.02). In this material I used several observations (only one per period) of the same pair as independent observations, so the sample resembles the colonial situation, but not all pairs were visited more than once, so the samples are not strictly comparable.

Individual variation in defence

The data suggest that in all species all the pairs intensify their defence behaviour as the season progresses.

Table 1. Percentage of pairs identified as attackers. Note that all pairs included here were given the opportunity to "prove" themselves as attackers, i.e. I included only pairs that were visited when they had chicks.

Species	Attackers (%)	Pairs
Great Black-backed Gull	54	11
Herring Gull	21	38
Common Gull	26	19

As the chicks hatch, the fraction behaving indifferently or at least inconspicuously decreases to about nil, and most become at least passive mobbers, joining a circling flock. Not all become active mobbers. Active attackers occur in all three species, but the behaviour seems to manifest itself only after chicks have hatched. One extremely aggressive pair of Great Black-backed Gulls attacked while still incubating, whereas the other aggressive pair of this species behaved very timidly while incubating. My records suggest that the percentage of active attackers differs between the species (Table 1, $\chi^2=4.8$, $df=2$, $P=0.09$). In Table 1, I have included only pairs that had had the opportunity to "prove" themselves as attackers, i.e. those whose chicks I handled. Other data collected by me during the chick stage in eight Herring Gull colonies (including the study colony) using the zig-zag walk through most territories in them suggested that the attack rate of was high in the study colony. Thus the actual number of attackers in the total population may be lower than that in Table 1.

I found no relationship between colony size and attack rate in these eight colonies ($r_s=0.34$, $n=8$, ns), which indicates that colony size alone may not reflect how hostile the colony is to a human intruder. In these colonies the attack rates varied between 0 and 1 per minute (mean 0.26 ± 0.34), and the flock size between 32 and 120 birds (mean 59 ± 29).

The numbers of attacks per minute delivered by individual pairs identified as attackers varied significantly between species (Kruskal-Wallis test, $H=6.75$, $df=2$, $P<0.05$, Table 2). Common Gulls seem on the average to have a higher attack frequency, probably due to their smaller size and better manoeuvrability. In the case of a human intruder, Common Gull attacks are more annoying than effective, whereas close attacks by Great Black-backs and Herring Gulls have to be taken seriously. The effect on real predators is unknown.

Table 2. Attack rates of identified attackers (per minute) in the three species. The observations were made when the chicks were aged about 2 wk in the larger species, and about 1 wk in the Common Gull. For each pair, I first located the chicks and handled (ringed) them, but did not let them run amok.

Species	No. of attacks (mean±SD)	Obs. time (mean±SD)	Total time (min.)	Pairs
Great Black-backed Gull	2.7±1.2	4.8±1.7	33.5	7
Herring Gull	3.2±3.1	2.2±0.9	22.2	10
Common Gull	9.7±6.4	1.2±0.9	6.0	5

Discussion

Defence behaviour

Aerial mobbing coupled with anxiety calls and also involving direct attacks occurs in a number of *Larus* species (see Conover 1987, Kruuk 1964, 1976). The distraction displays described here seems very rare. Kruuk (1964) described one form of them in the Black-headed Gull, and other species showing distraction displays are Sabine's Gull *Xema sabini*, Franklin's Gull *L. pipixcan*, Brown-hooded Gull *L. maculipennis* and the Common Gull (see Gochfeld 1984). Vermeer & Devito (1986) reported that a distraction display was commonly used by solitary nesting Common Gulls at Kennedy Lake, Canada. This study shows that distraction displays are sometimes used by colonial Common and Herring Gulls, but they were never observed in solitary Great Black-backs.

Defence behaviour in relation to breeding stage

It has recently been hypothesized that parent birds are more willing to defend older offspring (Andersson et al. 1980). This idea implies that the birds behave differently at different stages of the breeding cycle. The present study suggests that in all three species behaviour is more extreme during the chick phase than during incubation in all three species. Intensification of defence as the season advances has already been suggested for Herring Gulls (Burger 1984, Kilpi 1987a), Black-headed Gulls (Kruuk 1964), Sandwich Terns *Sterna sandvicensis* (Veen 1977), Arctic Terns *S. paradisaea* and Common

Terns *S. hirundo* (Lemmetyinen 1971). The list of waders showing a change in defence behaviour between incubation and chick-rearing is extensive (Gochfeld 1984). Knight & Temple (1986) pointed out that an apparent increase in defence may simply reflect loss of fear in the study object. Montgomerie & Weatherhead (1988) recently showed that the arguments of Knight & Temple (1986) were not entirely justified, and that in some species habituation clearly does not account for changes in defence behaviour as the season progresses. Many of the changes between incubation and chick rearing involve more risk taking by the parents during the latter stage. Direct attacks on the intruder are risky for gulls (Conover 1987), and injury feigning when rearing chicks renders many waders very conspicuous to predators, in contrast to their inconspicuous appearance when incubating (Gochfeld 1984). There can thus be little doubt that more risks are taken to protect chicks than eggs.

The difference in attack rates in the two Common Gull colonies studied here is probably due to differences in breeding success. In the colony having higher rates of attacks breeding was exceptionally successful (1.3 fledged young/pair), while in the other colony it was exceptionally poor (0.08 fledged young/pair) due to heavy predation by Herring or Great Black-backed Gulls. As the pairs lost their chicks, also an increasing fraction probably lost the motivation for defence. Production in the Herring Gull colony was very high (2.0 fledged/pair), and all Great Black-back pairs visited during the chick stage fledged at least one young.

Mobbing behaviour and coloniality

My records suggest that solitary Great Black-backs attack more frequently than colonial Herring and Common Gulls. Communal mobbing in colonies is often assumed to be one of the advantages of colonial breeding (Wittenberger & Hunt 1985). Strange Great Black-backs were attracted to sites where the resident pair was mobbing me, but were frequently attacked by the site owners. The strangers did not attack me. The tendency for one bird of a pair to stay circling above the site may be an adaptation to dealing with strange gulls attracted to the site. Thus it seems that solitary Great Black-backs deliberately prevented communal mobbing, and solitary pairs may be hypothesized to invest more energy in defence than colonially breeding pairs, since they attack both the

intruder at the nest and strange gulls attracted by the mobbing. The hypothesis could be tested in areas where both breeding strategies exist.

But did communal defence exist in the colonies? Communal defence in Common Gulls has been claimed to improve breeding success (Götmark & Andersson 1985). I found no correlation between flock size and attack rate, which suggests that no direct benefit of this kind is obtained from nesting in groups in this respect. Similarly, Götmark & Andersson (1984) did not find any indication that defence was better in large than in small colonies of the Common Gull. In the present study attacks were delivered by specific pairs in specific territories, and there was considerable variation in the defence behaviour of individual pairs. There was no indication of active participation of neighbours in active mobbing within the colonies (see Wittenberger & Hunt 1985). The term communal defence incorporates a notion of mutual "helping" in defence, which I could not observe.

In my study colonies some pairs were willing to invest more in defence and take greater risks (the attackers), than the other pairs (passive mobbers). Passive mobbers have been regarded as non-breeders (Conover 1987), but in my colonies passive mobbers included pairs with as much at stake as the attackers. It seemed that the pairs defended their own investment with varying intensity, and attacks might be made in one part of the colony, but not in another.

For deterring predators, a good strategy would be to breed close to an attacker, since attacks are usually triggered only near the territory of that pair. Joining the mobbing flock as a passive member did not seem to serve as a predator deterrent.

Kruuk (1976) suggested that flocking provides information about the predator, a hypothesis also put forward by Conover (1987). I suggest another function of passive mobbing. Neighbours are a serious threat to offspring especially in large gulls (Burger 1984 and references therein). Therefore it is clearly advantageous to be able to return synchronously to the colony after disturbance (see also Kilpi 1987a). A synchronous return is aided by knowing what is happening in the colony, and joining the mobbing flock is a better option than being in a place from which it will take longer to return. Thus, mobbing may be an adaptation to the colonial breeding strategy rather than one of the reasons for it.

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Selostus: Jälkeläispuolustukseen liittyvä käyttäytyminen ihmistä kohtaan meri-, harmaa- ja kalalokilla

Tutkin kesällä 1987 jälkeläispuolustukseen liittyvää käyttäytymistä merilokilla (yksittäispesijöitä), harmaa- ja kalalokilla (molemmat koloniaspesijöitä) Hangon edustalla. Poikasten ollessa pieniä kaikki kolme lajia joko kiertelevät pesimäsaaren yllä (passiivinen simputus) tai hyökkäävät kohti tunkeilijaa (suora simputus). Hyökkäykset eivät yleensä johda kosketukseen, sillä vain muutama yksilö kaikilla lajeilla iski jaloilla tunkeilijaa. Harmaa- ja kalalokilla esiintyi myös harhautuskäyttäytymistä, jolloin lintu lentää vaappuen matalalla, joskus jalvoja roikottaen, ikäänkuin johdatellen tunkeilijaa pois pesimäpaikalta. Tulokset viittaavat siihen, että poikasaikaan emot ovat aktiivisempia puolustuksessaan kuin haudonta-aikana. Hautovat merilokit kiertelevät korkealla luodon yläpuolella, usein ääneti. Molemmat muut lajit laskeutuvat usein mereen odotellen häirinnän päättymistä, kun taas merilokki ei tee tätä. Poikasaikaan höykkäykset yleistyvät. Merilokit tuntuvat olevan useammin höykkääviä kuin harmaa- tai kalalokit. Höykkäilyvyys vaihtelee suuresti parien välillä, ja kolonioisakin vain osa pareista suorittavat syöksyjä. Yhdyskunnissa en pystynyt osoittamaan mitään yhteistoimintaa puolustuksessa, yhteispuolustus tuntuikin olevan illuusio, joka johtuu monen parin pesimisestä lähekkäin. Ehdotan, että kookkaille lajeille, kuten harmaalokille, on edullista pysytellä lähellä omaa reviiriä häirinnän aikana siksi, että samanaikainen laskeutuminen häirinnän päätyttyä on eduksi, koska sillä tavoin voidaan välttää naapurien aiheuttamat tappiot. Näin ollen simputus saattaisi joissakin tapauksissa olla tärkeä sopeuma koloniaalisuuteen, mutta ei syy siihen.

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