Do Herring Gulls (*Larus argentatus*) invest more in offspring defence as the breeding season advances?

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The behaviour of Herring Gulls breeding in a colony in southern Finland was observed in 1986. A standard procedure was used to drive the birds from the colony and their subsequent behaviour was recorded. As the season advanced, an increasing number of adults engaged in harassing the intruder and the birds returned more rapidly to the colony (the measured variables were the times taken for the first bird to settle, for the last bird to leave the water, and for all the birds to settle). The adults returned more rapidly during the small-chick phase (up to the time the first chicks escaped into the water) than during incubation, which is suggested to be an important adaptation to reduce intraspecific predation. The results suggest that adults invest progressively more in offspring defence as the season advances and the value of the offspring increases.

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Introduction

All parental behaviour during nesting and raising of offspring can be expected to be related to a trade-off between maximizing the survival of the adult and the survival of the offspring. In species with parental care, adults may improve offspring survival by defending them against predators (Kruuk 1964). In many bird species investments in defence have been argued to increase as the season advances (Barash 1975). This could be based on cumulative parental investment, since the relative difference between the expected survival of parent and offspring decreases as the offspring grow, making parents more willing to defend older offspring (Andersson et al. 1980). The hypothesis of increasing parental investment (Barash 1975) has been developed for altricial species, but could be extended to semi-precocial species such as the Herring Gull (*Larus argentatus*) whose chicks spend a prolonged period within the territories (see Burger 1984).

In large colonies of Herring Gulls, intraspecific predation and killing of chicks may pose a severe threat to chicks (Parsons 1971, Hario 1985, Hunt & Hunt 1976). If, as suggested by Andersson et al. (1980), parents defend older chicks more vigorously, then behaviour relating to offspring defence should increase in colonial Herring Gulls as the season advances.

Burger (1980, 1984) has demonstrated that the aggression level in breeding Herring Gulls varies with the season. She detected a marked increase in aggressive behaviour after the chicks hatched. In the Herring Gull defence of offspring against predators from outside the colony could thus increase in the course of the season. There might also be a detectable overall change in parental investment around the time of hatching in response to intraspecific threats in the colony. Since Herring Gull colonies are usually synchronous in breeding (Gochfeld 1980), most birds should change their behaviour at the same time.

In this study of investment in chick defence by the Herring Gull, I examined behavioural variables chiefly related to avoiding intraspecific threats, such as synchronous settling after a severe disturbance, to test whether a seasonal trend in overall investment is present.

Material and study area

The data were gathered during the breeding season (May–July) in a colony off Hanko, SW Finland (approximately 60°N 23°E) in 1986. In the colony 35 pairs were nesting in a tight cluster, the mean nearest-neighbour distance being 3.3 m (SD 1.3). The colony was visited 22 times during the breeding season. I landed each time at the same spot, chased off all the birds and stayed on the island for about 30–60 minutes. The behaviour of the adults was recorded for about 10 minutes after my arrival (number settled on the water, number in the air above the colony). When leaving the colony, I entered my boat, and once the motor was running, made sure that most birds were able to see that I was leaving, and started timing the events with a stopwatch. I drove about 150 m away from the island and observed the return of the adults until all the birds had settled, and then watched the birds for a three-minute period. I noted (1) when the first bird arrived above the colony, (2) when the first settled, (3) when the last left the sea-surface and (4) the time it took for all birds to settle. All fights during the return and the following three-minute period were also recorded. The breeding phenology of the colony was established by regular counts of nests every second or third day throughout the season. All visits were made at approximately the same time in the morning (09.00–11.00) in favourable weather.

Results

General behaviour of the parents during disturbance

During early incubation, the birds rapidly left the colony, and after a few minutes had usually all settled on the water, forming a fairly aggregated raft some 150–200 m away. After the first few minutes birds very seldom flew about over the colony uttering alarm calls. When I had left the shore in my boat, the first bird arrived over the colony in a few seconds. My impression was that the behaviour of the birds changed as incubation progressed, becoming less timid towards the intruder, but I have no quantitative data to support this impression, since too few counts were taken during incubation.

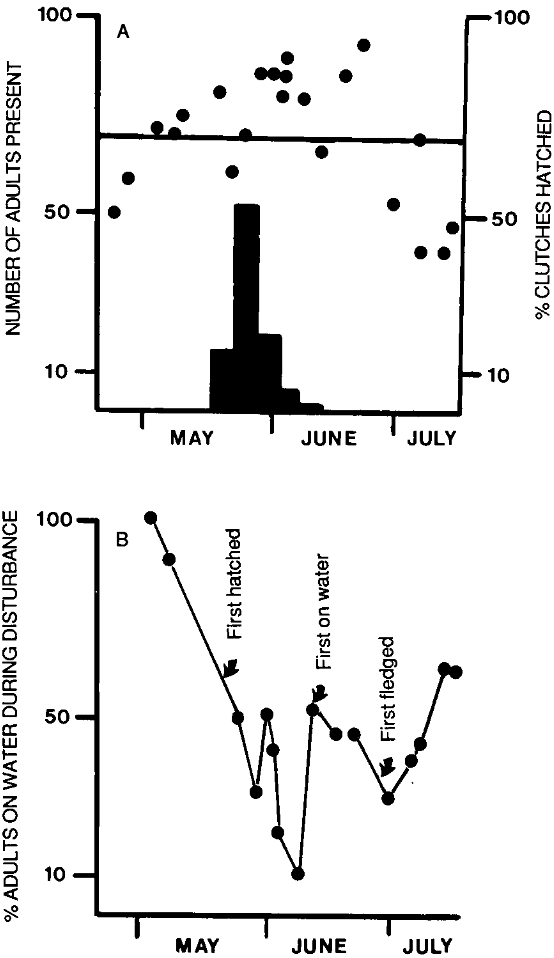

Fig. 1. Graph A gives the number of adults present in the colony during the 1986 season (black dots, scale to the left), and percentage of clutches hatched (histogram, scale to the right). The line gives the maximum number of adults expected if all breeders were present. Percentage of adult birds swimming on the water during the disturbance (graph B). The main events relating to breeding are indicated by arrows.

Table 1. Time variables related to the return of Herring Gulls to the colony after disturbance determined on 12 visits. The Spearman rank correlation coefficient gives their relation to the date up to the time when the first chicks escaped into the water. All correlations are highly significant (P<0.001; see text).

Time passing	Seconds	Spearman r_s
Before first bird settles	45– 95	–0.77
Before last bird leaves water	25–130	–0.76
Before all birds settle	85–205	–0.92
Between settling of first and last bird	30–145	–0.75

The behaviour of the adults changed decisively during the time when the chicks were young (see Fig. 1). The birds resorting to the sea surface gradually decreased to a very few and there was a constant flock of alarmed birds above the colony harassing me, without any time gap between my departure and the arrival of the first bird above the colony (6 occasions, up to 19 June). The continuous decline of adults on the water during the first eight counts (Fig. 1) was highly significant (Spearman rank correlation r_s = 0.881, df = 6, $P < 0.001$). Thus increasingly more energy was put into direct defence of the offspring.

As chicks started to enter the water during the disturbance, they were joined by an increasing proportion of adults. Around the time when the first chicks fledged (first observed on 29 June), unfledged chicks were joined by their parents on the water in discrete family groups. Later, when a large proportion of the young had fledged, this behaviour was not so clear, since the fledged chicks tended to form flocks of their own. Thus unfledged chicks were guarded closely when they were on the water, but fledged chicks were not so carefully protected.

The number of adults attending the colony at the time of my visit rose as incubation advanced, reaching a high level just before the first chicks fledged, after which it declined (Fig. 1A). During the peak the number of adults on several occasions exceeded that predicted by the size of the colony (35 pairs, 70 adults), suggesting that non-breeding prospectors had arrived, which increases the risk of predation.

Settling in the colony after disturbance

The pattern of return to the colony was studied on 12 days up to the time when the first chicks took to the water during disturbance. All the measured variables decreased significantly throughout the season (Table 1), indicating increasingly rapid return.

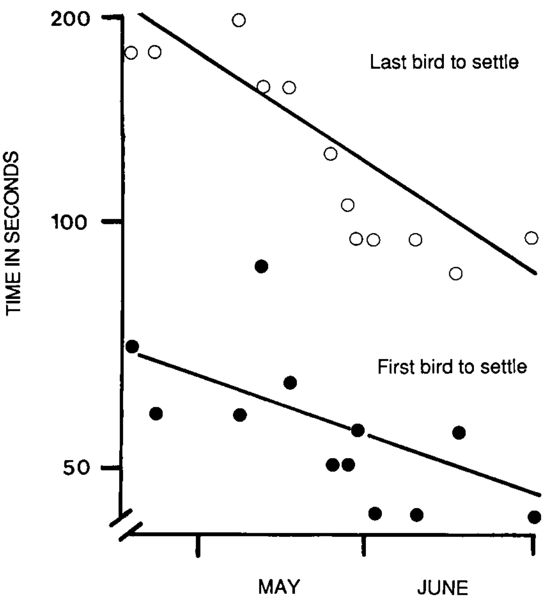

Fig. 2. Time (in seconds, log scale) passing before the first (black dots) and last bird (open circles) settled in the colony after the disturbance.

In order to check whether there were any differences in the trends, I further examined the seasonal trend for the first bird to settle and the last bird to settle (Fig. 2). The correlations were both significant ($r=-0.64$, $df=10$, $P<0.025$ for the first bird to settle, $r=-0.88$, $df=10$, $P<0.001$ for the last bird to settle). A problem with statistical tests of the present kind of data is that there are no distinctly defined sample units. In theory, it is possible that the first bird to land in the colony was always the same, in which case I am testing for changes in the behaviour of a single individual. This problem can be avoided only by marking and observing a number of different individuals. Tests of significance may thus formally not be appropriate in the present context, or in Tables 1 and 2. I regard this theoretical consideration as relatively unimportant in practice, as the birds settling first and last did not always settle on the same territories. More importantly, the slopes in Fig. 2 are

Table 2. Means (in seconds, ± SD) for the time variables describing the return of Herring Gulls to their colony after disturbance, and the significance of the differences between the incubation (n=6) and small-chick (n=6) phases (Mann-Whitney U-test).

Time passing	Incubation	Small-chick	P
Before first bird settled	66.5±14.7	49.2±4.9	<0.01
Before last bird leaves water	84.7±26.9	47.5±21.6	<0.025
Between settling of first and last bird	99.5±28.1	40.0±7.1	<0.001

significantly different, when 95 % confidence limits are constructed for the regression coefficients (T' method according to Sokal & Rohlf 1981). Thus the time elapsing between the settling of the first and last bird decreases more rapidly than does the settling time of the first bird.

Because my observations suggested a clear change in behaviour between incubation and the small-chick phase, I divided the data further into two blocks (Table 2). Settling times were shorter during the small-chick phase than during incubation (all differences statistically significant). Thus it seems that when the chicks are small, the birds return to the colony more rapidly and synchronously, which is reflected by the smaller standard deviations (see Gochfeld 1980).

Fighting

Fighting was rare. Birds landed directly on their territories, and during the three-minute watch after all the birds had settled, the scene generally appeared very peaceful. In all, only seven clashes (short displacement attacks on the landing bird by the presumed territory-owner) were seen during 36 min of observations. All these clashes occurred on two occasions (30 May and 8 June) when most of the chicks were small. Only one almost fledged chick was found killed during the whole season.

Discussion

The observations indicate that the overall behaviour of the parents changes during the breeding season. Parents become more aggressive towards intruders when hatching is near, and the numbers of adults present over the colony during an intrusion grow progressively until chicks begin to leave the colony when disturbed. Defence was here defined in a simple manner by taking the proportion of adults engaging in attacks and alarm behaviour above the colony, but nonetheless it seems to support the prediction that investment increases as the breeding season progresses. Lemmetyinen (1971) found a similar increasing trend in aggression towards an intruder in Arctic and Common Terns (*Sterna paradisaea, S. hirundo).* A seasonal increase in defence behaviour has been documented in a number of species (Andersson et al. 1980, Barash 1975, Lemmetyinen 1971), including the Herring Gull (Burger 1984).

The behaviour related to guarding eggs or chicks in the colony, namely rapid return to the colony and rapid settling on the territory also changed with time. Settling was not as synchronous during incubation as when the chicks were small. The data indicate that behaviour changed rapidly once the chicks had hatched. This is in accordance with the prediction made, and probably a response to the greater hostility of the environment to chicks. Burger (1980) found that Herring Gulls started expanding their territories once the chicks had hatched, and that levels of aggression in the colony peaked at this time. The more hostile environment would render effective guarding and defence of chicks advantageous.

Recently, Knight and Temple (1986) argued that the increased defence found in many studies is a methodological artifact. They suggest that when an observer repeatedly visits a nest, the defence behaviour is gradually modified by positive reinforcement and loss of fear. This is clearly a problem in this type of study. The settling of the first bird could easily be affected in such a way. Positive reinforcement may be disproved by the fact that the interval between the settling of the first and last bird contracts as the season advances (Fig. 2). The time taken by the first bird to settle is about 36 % shorter during the small-chick phase than during the incubation phase (calculated from the means in Table 2), but when the first-to-last bird interval is considered, the decrease is 60 %. I would interpret this as a real tendency for the birds to return increasingly rapidly and not as the result of positive reinforcement. The settling of the rest of the birds after the first bird has settled should not be affected by the observer, but rather it should be seen as a process triggered by the settling of the first bird. The observations were made at a distance not normally causing any distress to the birds in the colony.

The risk of losing a chick is probably higher than the risk of losing an egg. Eggs, with their cryptic coloration, are better protected against predation. Hario (1985) found that well-nourished chicks of the Lesser Black-backed Gull (*L. fuscus*) were more susceptible to predation by Herring Gulls, because they moved more than undernourished chicks. Hunt and Hunt (1976) also showed that the chicks of Glaucous-winged Gulls (*L. glaucescens*) which moved most were also the most prone to risks.

In my study colony, few eggs were lost during incubation. In 1986, 113 eggs were laid, of which 8.8 % were lost. Small chicks disappeared more frequently (18.5 % of the 92 successfully hatched chicks). Small chicks are more vulnerable than large chicks (Burger 1984, Hario 1985).

According to my own, albeit qualitative, observations, chicks that leave the colony when disturbed (at the age of about three weeks) are at first defended and guarded on the water. As they begin to form flocks, they are gradually left unguarded, which suggests a drop in defence investment once the young are fledged.

In Fig. 3 my observations are fitted to the model suggested by Andersson et al. (1980). My observations during the incubation and small-chick phase fit well with the predictions made by Andersson et al. (1980). The curve I have drawn is based on their data on the Fieldfare (*Turdus pilaris*) in which defence seems to level off as the chicks approach fledging age. Burger (1984, curve b in Fig. 3) suggested that defence should bear a relation to the direct threat to the chicks' existence, decreasing as the chicks grow

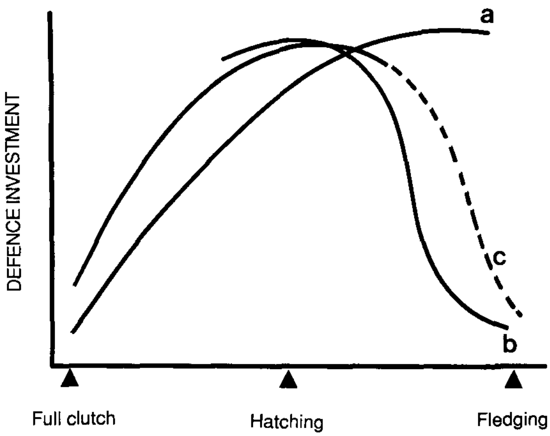

Fig. 3. The relation between offspring defence and the age of the "offspring" from full clutch to fledging according to Andersson et al. (1980) (curve a), Burger (1984) (curve b) and my interpretation of my own observations in this study (curve c).

older. I suggest a similar decrease in the Herring Gull (curve c in Fig. 3). The older chicks escape into the water, and the threat posed by neighbours thus decreases.

In Finnish Herring Gulls the time available for raising offspring is limited, since the environment becomes gradually unfavourable in autumn, as is evident from the fact that the birds migrate (Kilpi & Saurola 1983, 1984). Normally the colonies are abandoned in mid-July, and the juveniles move independently in early August (Kilpi & Saurola 1983, Kilpi unpubl.). Clutches lost early in the season may be replaced, but Herring Gulls seldom lay replacement clutches if chicks are lost (own data). Time is a limiting factor in this respect, and the farther the season advances, the more valuable the offspring become. The present results seem to indicate that the investment in keeping the offspring alive also increases.

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Selostus: **Sijoittavatko harmaalokit enemmän jälkeläisten puolustamiseen pesimäkauden kuluessa?**

Seurasin kesällä 1986 pesivien harmaalokkien käyttäytymistä Hangon edustalla. Häiritsin lintuja säännöllisesti nousemalla yhdyskuntaluodolle maihin läpi pesimäkauden. Pyrin joka häirintäkerralla käyttäytymään samalla tavalla, ja merkitsin muistiin, miten vanhat linnut käyttäytyivät, miten suuri osa niistä jäi veteen ja miten suuri osa niistä hyökkäili minua kohti (kuva 1). Poistuessani mittasin miten pitkään kesti ennen kuin (a) ensimmäinen lintu laskeutui, (b) viimeinen lintu nousi vedestä ja (c) viimeinenkin lintu laskeutui yhdyskuntaan.

Aikuiset harmaalokit muuttuivat hyökkäävämmiksi haudontakauden lopulla, ja ne olivat hyvin hyökkäileviä aina siihen saakka, kunnes poikaset noin kolmen viikon ikäisinä alkoivat sännätä uimasilleen käyntieni aikana. Pesimäkauden edetessä ensimmäinen lintu laskeutui yhä nopeammin yhdyskuntaan häirinnän jälkeen, viimeinen lintu nousi yhä nopeammin vedestä ja samoin viimeinen lintu laskeutui yhdyskuntaan yhä nopeammin (taulukko 1). Pesimäkauden edetessä siis paluu oli yhä nopeampaa, ja kaikkien lintujen asettuminen oli myös nopeampaa ja synkronisempaa (kuva 2). Taulukossa 2 tätä on tarkasteltu erikseen haudonta-aikana ja poikasten ensimmäisten elinviikkojen aikana.

Nopea paluu yhdyskuntaan häirinnän jälkeen on tärkeä sopeutuma yhdyskuntapesintään. Yhdyskunnassa munat ja varsinkin pienehköt poikaset saattavat joutua naapureiden syömiksi tai tappamiksi, joten jälkeläisten puolustamisen takia emojen on oltava paikalla mahdollisimman yhtäaikaisesti muiden lintujen kanssa. Yhdyskunnissa oleskelevat pesimättömät linnut saattavat myös uhata poikasia, ja niitä ilmestyi paikalle huomattavia määriä juuri poikasten kuoriutumisen aikaan (vrt. kuva 1). Käyttäytyminen muuttui poikasten varttuttua niin vanhoiksi, että ne eivät enää jääneet yhdyskuntaan, vaan pakenivat mereen.

Tarkastelen tuloksia suhteessa teorioihin, joiden ennusteiden mukaan aikuisen linnun tulee sijoittaa sitä enemmän aikaa ja energiaa jälkeläisten puolustamiseen mitä arvokkaamaksi (vanhemmaksi) ne tulevat. Mitä pidemmälle pesimäkausi edistyy, sitä arvokkaammaksi ja samana kesänä korvaamattomammiksi jälkeläiset tulevat. Harmaalokki pystyy korvaamaan menetetyn munapesän, mutta harvemmin menetetyn poikaskatraan. Tämän takia sijoittaminen puolustukseen on tärkeää. Tulokset tukevat ennusteita (kuva 3).

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