Ornis Fennica 71:1–10. 1994

Reproductive performance of the nominate Lesser Black-backed Gull under the pressure of Herring Gull predation

Martti Hario

Hario, M., Finnish Game and Fisheries Research Institute, Game Division, P.O. Box 202, FIN-00151 Helsinki, Finland

Received 28 December 1993, accepted 14 April 1994

Predation by Herring Gulls *Larus argentatus* was one of the major causes of death among Lesser Black-back chicks *Larus f. fuscus* during a 14-year study period in the Gulf of Finland. Prior to culling operations, 17% of chick deaths were attributed to predation by neighbouring Herring Gulls in the study colony (chicks' rings were found in predators' food remnants). Culling these proven predators (2 pairs) lowered the predation rate to 2% and improved the fledging result significantly. However, predatory gulls from adjacent colonies, operating also in the study colony, were harder to track and remove. This "long-distance" predation still continued to operate even though the numbers of occupied Herring Gull nests in the entire Söderskär archipelago were reduced by 40% in four years (by egg culling). Hence, random culling is not an effective solution in cases when selective removal of every specialized predator is not possible. This report does not, however, aim to asses the ethical grounds and the legitimacy of culling programs. Despite being a relatively large gull with a relatively large territory size, the nominate race of the Lesser Black-backed Gull shows behavioural analogies to the smaller, inoffensive gulls. It shows no intraspecific predation, and lacks effective defence against interspecific predation by larger gulls. Therefore the nominate *fuscus* seems to be especially vulnerable to Herring Gull predation. At present, the predation has an adverse effect on the reproduction of the nominate *fuscus* as it applies predominantly to the best-growing chicks, the potential recruits of the population.

1. Introduction

The great decrease in the population of the nominate race of the Lesser Black-backed Gull (*Larus f. fuscus*) in Baltic coastal areas has provoked discussion about the role played by increases in Herring Gull (*Larus argentatus*). Herring Gulls are said to displace Lesser Black-backed Gulls in territorial clashes on breeding grounds (Paludan 1951, Bergman 1965, 1982, Kilpi 1983). There are also numerous indications that Lesser Black-back chicks are preyed on by Herring Gull adults (Paludan 1951, Hario 1981, Bevanger & Thingstad 1990). Cannibalism or infanticide have never been reported in the nominate Lesser Black-backed Gull in contrast to the western race *graellsii* (e.g. Davis & Dunn 1975). Nominate *fuscus* is also considered more specialized in its feeding biology than *graellsii* and *L. f. intermedius*, and it also shows clear dif-

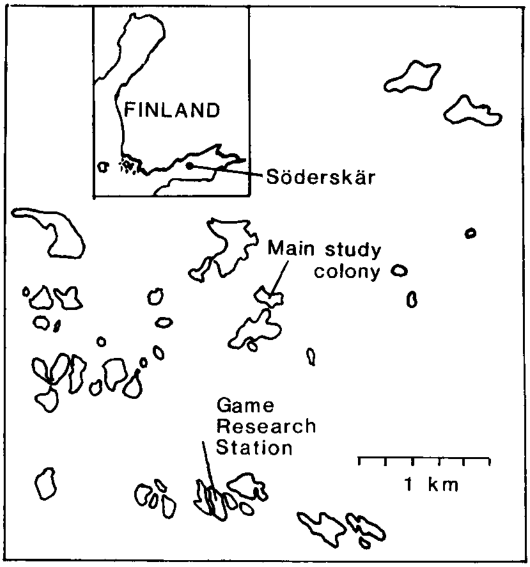

Fig. 1. Location and map of islands at the Söderskär bird sanctuary.

ferences in morphology, migration route, moulting cycle, population parameters and population development, and may even be specifically different from *graellsii* and *intermedius* (Strann & Vader 1992).

In this paper I describe the vulnerability of the nominate *fuscus* to Herring Gull predation. I also discuss the mechanism by which Herring Gull displaces Lesser Black-backed Gulls on the breeding grounds. Throughout this paper I examine only the nominate race of the Lesser Black-backed Gull (*L. fuscus fuscus*); this form is nowadays regarded as "endangered" in the Red Data Books of Estonia, the St. Petersburg region, Finland, the Åland Islands, and Norway, i.e. over most of its range.

2. Material and methods

The study was made at the Söderskär bird sanctuary which lies about 25 km southeast of Helsinki, in the outer archipelago of the central Gulf of Finland (60°07′N, 25°25′E; Fig. 1). It consists of 25 small rocky islets with some elevated patchy grassy vegetation and dense juniper cover in the central parts. Four of the islets are partly wooded with stands of aspen and spruce; they average 3.35 ha in size, the rest are treeless skerries, 1.14 ha on the average. The total land area of the sanctuary is about 0.5 km^2, and water area 13.3 km^2. The sanctuary is rich in seabirds (protected since 1930), with gulleries and terneries of various sizes on every islet (Hario et al. 1986).

The main study colony breeds on a treeless islet (1.3 ha) with dense grass vegetation. In 1980–93, nests were marked and mapped as soon as they were located. Laying was surveyed on a nest-by-nest basis during visits at 1–3-day intervals. The fate of the chicks was monitored by daily visits, weather permitting, during the whole chick-rearing period up to the first week of fledging.

The chicks were ringed within 1–3 days of hatching, and their weight gain was monitored daily or whenever the chick was found; when older, the chicks hid among vegetation, and it was not possible to find every chick every day. In 1992–93, the distance the chick ran from the nest was measured from the nest to the chick's hiding place. The nearest-neighbour-distance of each occupied nest was measured in 1984, 1988, 1991 and 1992 in the study colony.

Predation was confirmed by locating rings of chicks in gull pellets and food remnants in surrounding territories and in nearby colonies. Systematic searches were conducted every year in the main study colony and in 1985, 1986 and in 1990–92 over most of the Söderskär area.

Predatory Herring Gulls and Great Black-backed Gulls (*Larus marinus*) were culled during 1985–90 under the licence of the Ministry of the Environment. The principal aim was to remove only the proven predators, but a larger reduction around the study colonies was felt necessary in 1987 and 1989, and 5.5% and 4.8%, respectively, of all breeding Herring Gulls at Söderskär were culled.

Egg culling was conducted in 1986–89 over the whole Söderskär area by removing the whole clutch and considerable efforts were put into finding all relayings. In the main study colony, Herring Gull eggs were culled by egg-pricking every year (1984–90).

The technique used in adult culling — that of placing a narcotic bait in the nest — has been described elsewhere (Stenman et al. 1972).

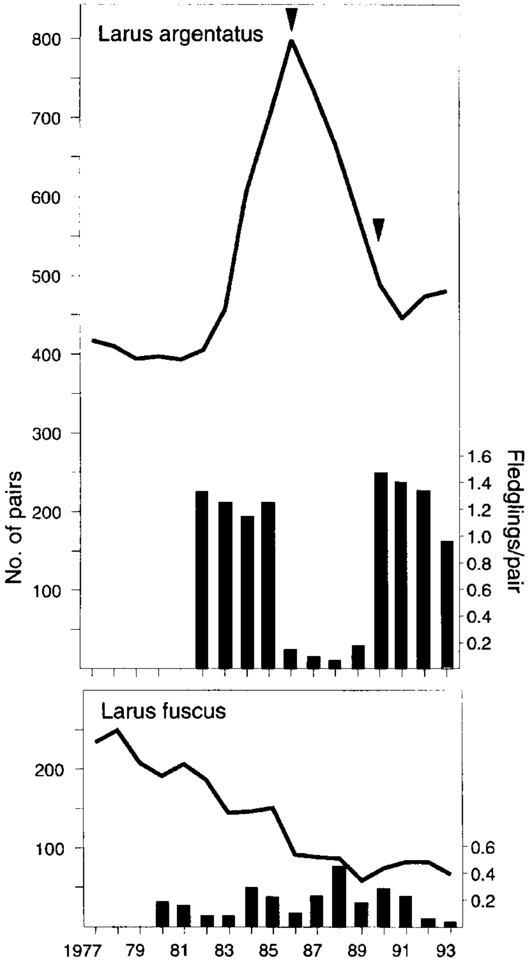

Fig. 2. Population trends of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*Larus fuscus*) at Söderskär in 1977-93 (no. of pairs, graphs). Bars indicate the mean numbers of fledglings per nest in different years (scale to the right). Arrows give the period of egg culling on Herring Gulls (1986–89).

3. Results

3.1. Population trends and overall breeding success

Throughout the Söderskär area, the decline of Lesser Black-backed Gulls averaged 11% per annum during 1978–93 (Fig. 2). In 1983, 1986, 1989 and 1993, the numbers declined steeply by 23, 39, 33 and 20%, respectively.

The fledging rates during 1980–93 varied between 0.03 and 0.45 (annual means) averaging 0.18 fledglings per clutch (SD = 0.11; annual no. of clutches is analogous to the annual number of pairs in Fig. 2).

The populations of Herring Gulls were markedly affected by the culling operations. First, an increase by 19% per annum took place during 1983–86 (Fig. 2). At its height the population consisted of 798 pairs in 1986. Continuous egg culling during 1986–89 and the two small-scale culling operations of adults in 1987 and 1989 depressed the numbers (489 pairs in 1990, a 10% decline per annum). From 1991 on, the numbers have increased again.

Relaying following egg culling was comparatively high among the Herring Gulls; in 1988 and 1989 the proportion of relayed clutches was 52% and 19% of the initial number of nests, respectively. Although several repeated egg cullings were conducted annually, the population managed to raise on average of 0.12 fledglings/pair during 1986–89 (range 0.06–0.17, Fig. 2). Hence, it was impossible, in practice, to locate every nesting attempt in the 15 or so Herring Gull colonies at Söderskär, and every year several tens of pairs with offspring remained unnoticed until fledging. However, this was markedly less than in three reference areas in nearby archipelagos, where a single egg culling at the end of incubation period in 1988 resulted in fledging rates of 0.20, 0.37 and 0.38 (the corresponding figure for Söderskär area in the same year was 0.06).

The fledging rate for Herring Gulls was normally far better than that of the Lesser Black-backs, viz. on average 1.23 (SD = 0.13) in 1980–85 and 1.29 (SD = 0.23) in 1990–93 (annual sample sizes analogous to pair numbers in Fig. 2).

3.2. Culling results and chick losses in the main study colony

In the main study colony, two pairs of Herring Gulls (or at least one partner) took at least 17% of Lesser Black-back chicks (Table 1) and 8% of their conspecific chicks (Hario 1989) in 1980–84. This was verified by locating chick rings on the Herring Gull territories. Most of the chicks were downy young and taken whole. The remnants usually consisted of the ring and some down in the pellets. It would have been impossible to determine their fate without ringing and ring recoveries.

After culling the two pairs of Herring Gulls in spring 1985 and one pair in 1987 (also proven predators) predation pressure was temporarily reduced resulting in significantly higher reproductive success of Lesser Black-backs in 1985–90 (Table 1). However, the predation pressure increased again and the fledging result decreased concurrently when no culling on eggs or adults was conducted in 1991–93.

3.3. Long-distance predation

Despite the fact that the neighbouring Herring Gulls lost their clutches every year from 1984 on and their numbers were gradually reduced to 3 pairs (in 1990), the predation on Lesser Black-back chicks in the main study colony did not cease altogether (Table 1). This was largely due to predatory Herring Gulls from nearby colonies operating in the main study colony and other Lesser Black-back colonies as well (Fig. 3). In 1985, there were 5 such Herring Gull pairs on 212 territories surveyed, i.e. 4% of all. In 1986, the number was 6 of 300 territories (2%). These represent cases where Lesser Black-back chick rings (n = 22) were located in the Herring Gull territories. The flight distances between the predator's territory and the colony from which the chick(s) originated ranged from 300 m to one kilometre (Fig. 3).

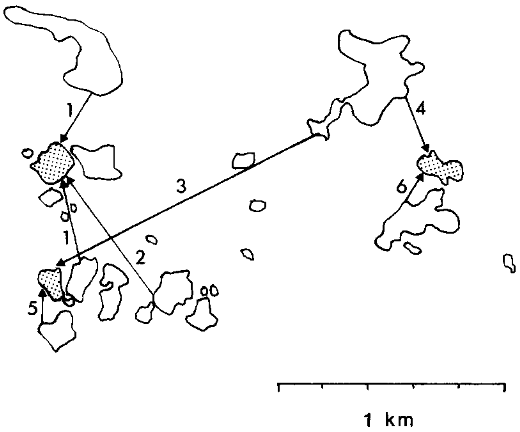

Fig. 3. The occurrence of long-distance predation in the Söderskär archipelago in 1986-93 (for the location, cf. Fig. 1). Arrows give the islands from where the predatory gulls came to the three Lesser Black-back colonies under survey (hatched islands). Data are based on 22 recoveries of rings of Lesser Black-back chicks, no. of recoveries given along each arrow. Arrows are used only to indicate the islands, not the actual numbers of predators.

Finding rings in long-distance predators' colonies was a laborious task because of the vast

Table 1. Causes of chick losses in the main study colony of Lesser Black-backed Gulls in years of predation pressure (= years with no culls, 1980-84 and 1991-93) and in years when the neighbouring predators were culled (1985-90). Percentages of totals in parentheses. G-test gives the difference between year groups.

	No. of chicks	Verified predation: Taken by neighbouring predators	Verified predation: Taken by long-distance predators	Diseased & starved	Disappeared	Other causes	Tot. losses
No culls							
1980–84	187	31 (17)	..	38 (20)	98 (52)	5 (3)	172 (92)
1991–93	121	10 (7)	3 (3)	20 (17)	79 (65)	2 (2)	115 (95)
Tot.	308	41 (13)	3 (1)	58 (19)	177 (57)	7 (3)	287 (93)
Years of culling							
1985–90	158	5 (2)	3 (2)	27 (17)	81 (52)	8 (5)	124 (79)
		G = 14.322 P < 0.001	G = 0.666 NS	G = 0.213 NS	G = 1.622 NS	G=2.459 NS	G = 20.404 P < 0.001

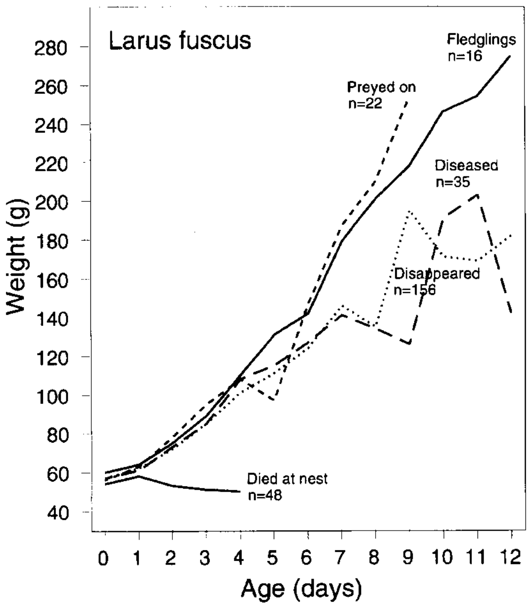

Fig. 4. Mean body weight of Lesser Black-back chicks according to age at Söderskär in 1991-93. Categories "diseased" and "died at nest" refer to chicks that died of inflammations and sepsis (verified at necropsy). The material stem from all the three study colonies (see Fig. 3).

areas, the often dense vegetation and the gulls' habit of spending a lot of time outside their territories, e.g. on open rocks, where their pellets readily wash to the sea. Therefore I suspect that my verification of the long-distance predation in the main study colony (Table 1) as well as in the other two study colonies (Fig. 3) represents minimum figures.

3.4. Chick disappearances

The fate of the chicks that disappeared is of great interest: were they taken by predators or did they die of other causes, their carcasses remaining undetected? Their growth rates (body weight) in Fig. 4 reveal that the latter is the case. The daily body weight of "disappeared" chicks fluctuated in a similar manner to that of the "diseased" chicks (Fig. 4), deviating markedly from the steady growth of both the "preyed-on" chicks and those that subsequently fledged. This suggests that most of the missing chicks were weak or diseased chicks which died hidden in vegetation and remained undiscovered, in contrast to the verified diseased chicks that died at or close to their nests and were readily found. The marked fluctuation in both growth curves ("disappeared" and "diseased" in Fig.4) results from momentarily healthy chicks (with increasing body weight) and already sick chicks (with decreasing weight) simultaneously affecting the daily mean weights. In contrast, most preyed-on chicks were in good shape. Although chick diseases (inflammations and sepsis, Hario & Rudbäck in prep.) are numerically the most important mortality factors, the impact of Herring Gull predation is particularly damaging as it affects the best-growing chicks, the potential recruits of the population.

In an attempt to evaluate how many of the missing chicks were actually taken by predators and how many were lost through disease one needs to consider the 0–5-day-old chicks separately from the older ones. This is because it was not usually until day 6 that disease started to affect the weight gain of the survivors from the first "death wave" (the hatchlings that "died at nest" in Fig. 4, their mean age 2 days). The parallel growth curves of missing and preyed-on chicks on days 0–5 indicate that these were equally healthy chicks and probably equally prone to predation at that time. On days 0–5, eight out of the 22 preyed-on chicks (data in Fig. 4) or 36% were taken. Assuming this predation rate applied equally to the missing cohort as well, I estimate that 35 (36% of 98) missing chicks fell victim for predation before they were 5 days old. Hence, the total loss for predation in Fig. 4 data (n = 277 chicks) would be 35 + 22 chicks, i.e. 21%. Diseases would then take 73% (121 + 48 + 35), and the number of fledglings (16) amounts to only 6% of the total chick production. This calculation actually underestimates predation because it makes the assumption that no missing chicks older than 6 days were taken by predators.

One further point needs to be stressed: no fledgling could escape detection and identification since all the half-flying birds could be readily recaptured, and their numbers were monitored closely upon their departure.

4. Discussion

4.1. Predation-induced mortality

Chick mortality caused by adult gulls can be divided into (i) territorial aggression and (ii) predation. Characteristically, predators eat chicks which they kill, while in territorial aggression the chicks killed are not normally eaten (e.g. Emlen 1956, Parsons 1971). These two mortality factors have been recognized in most published gull studies, with the former being much more common than the latter (for *Larus occidentalis*, see Hunt & Hunt 1975; *L. argentatus*, Paludan 1951, Brown 1967, Parsons 1971, 1975, Haycock & Threlfall 1975; *L. fuscus graellsii*, Davis & Dunn 1976; *L. marinus*, Butler & Trivelpiece 1981, Hudson 1982; *L. dominicanus*, Fordham 1970; *L. ichtyaetus*, Kostina & Panov 1982). In some studies, however, intraspecific killing could not be strictly separated from cannibalism/predation (Harris 1964, Kadlec et al. 1969, Southern & Southern 1984).

In the present study only predation was involved. I base this conclusion on the following:

1) In the main study colony during 14 study years, no Lesser Black-back chick, live or dead, with injuries around the head was found nor any with signs of pecking, attributable to adult attacks (466 chicks were handled on 2 253 occasions).
2) No vicious attacks by Lesser Black-back adults on chicks were noted during 250 nest-hours of observation from a blind (see Hario 1990) although adults were commonly seen interacting with each other.
3) 11% of Lesser Black-back chicks (during the 14 study years) were proven to have been eaten by Herring Gulls. Several of the rings recovered were located far away from the original nest site. There was no possibility that these chicks had wandered by chance to the predator's territories as the sites were isolated by sea or steep rocks from the predator's colony or subcolony.
4) Scavenging dead chicks was uncommon among Herring Gulls. Of the 42 chicks found dead in their colonies in 1992–93 (diseased/starved chicks) and left lying in the terrain (instead of being taken to further investigations as usually), 10 (24%) subsequently disappeared and were probably picked up by scavengers. The rest of the bodies were decomposed in position. No rings were found in Herring Gull territories.
5) Chicks also disappeared from enclosures, which is attributable only to avian predation. In experiments in 1981, six Lesser Black-back nests were surrounded by chicken wire (Hario 1981). All the brood members subsequently disappeared, as in free-living broods, at the age of 2–12 days.
6) Rings were only found in Herring Gull territories and once, in 1988, in a Great Black-backed Gull territory, but never in Lesser Black-back territories.

4.2. Investigator-induced disturbance

In colonial, terrestrial-nesting larids disturbance leads to an increased frequency of territorial aggression, with repeated visits by investigators resulting in elevated mortality among chicks (Duffy 1979, Fetterolf 1983, Mousseau 1984). The problem results from increased rates of chick running and territory trespassing. The above mentioned studies were conducted in very dense Ring-billed Gull colonies (*Larus delawarensis*), and they refer solely to intraspecific killing (territorial aggression). To what extent disturbance can affect predation pressure in gull colonies is hard to assess. No studies exist on this topic. If the predators can take advantage of disturbance they might learn to take chicks from the disturbed colonies. However, chick defending adults may also become accustomed to repeated intrusions and return to nest quickly after human disturbance (Burger & Gochfeld 1983).

In Söderskär Lesser Black-back colonies, the average length of chick runnings during disturbance (the distance from the nest to the chick's hiding place) was similar among chicks subsequently preyed on (5.1±5.2 metres, median 3, n = 23) and those subsequently fledging (5.1±11.0, median 1, n = 21; Mann-Whitney test, P = 0.11). The same applied to chicks that subsequently disappeared (3.7±4.8, median 2, n = 150, P = 0.08), but it was significantly shorter for chicks that fell victim for diseases or starvation (2.3±3.5, median 0, n = 30, P = 0.005). The latter ones died close to or at their nests (being often too weak to move around). The result implies that the preyed-on chicks did not run farther away from their territories than the more successful chicks. Hence, running longer was not a valid response to disturbance among Lesser Black-back chicks. Instead, the nest location within the colony had more effect on the susceptability of chicks being taken by predators (see later) as well as the number of (presumably) good hiding places.

4.3. Final fledging rate and the displacement mechanism

Throughout the 14-year study period, the Lesser Black-backs in the main study colony suffered from heavy reproductive failure through parental failure (adults eating own eggs and neglecting chick feeding, see Hario 1990), diseases, and predation.

The low fledging result did not provide a recruitment sufficient to replace the annual adult mortality, and territories were left unoccupied. To maintain the 1980 population level (191 pairs) at Söderskär with, say, 10% annual loss of adults, Lesser Black-backs must produce a yearly cohort of 38 first-breeders (0.10x382). Assuming survival from first winter to maturity as 44% (as in the Caspian Tern *Sterna caspia*, the other long-lived African-migrant among Baltic seabirds, R. Staav in Cramp 1985), the fledging rate needed would be 0.45 (38/0.44/191). The mean fledging rate in the 80s was only half of this (see Fig. 2). Hence, the population could not maintain itself.

There was no evidence of non-breeding among the colony-attending adults (Hario 1989), this justifying the use of the number of active nests as the parameter of the population size. Also, interchange of breeding birds with other colonies in the Gulf of Finland is improbable as the closest major colonies, some 100 km away in the east, were declining at the same rate (Hario 1989).

Therefore I suggest that Herring Gulls were not actively displacing Lesser Black-backed adults in mixed colonies (e.g. by being stronger in territorial clashes); they simply took over the empty territories which fulfilled their habitat requirements. During their steady decline, the Lesser Black-backs maintained their territories on the colony islets and were never observed to have been forced to unsuitable (atypical) habitats.

4.4. Why are Lesser Black-backed Gulls vulnerable to predation?

As was shown by Götmark (1982), the Lesser Black-backed Gull takes the intermediate position in the degree of coloniality among the five Baltic-coastal *Larus* gulls (*marinus, argentatus, fuscus, canus, ridibundus*). According to Hunt & Hunt (1976), large body size allows for a large territory for growing chicks to find space and hide from the dangerous neighbours, i.e. from intraspecific killing and cannibalism (see also Burger 1981). Smaller larids have smaller territories, but no cannibalism. Instead, they suffer from a high degree of intraspecific killing, i.e. territorial aggression (see e.g. Emlen 1956, Patterson 1965, Burger 1974, Fetterolf 1983, Mousseau 1984).

According to the model of Hunt & Hunt (1976), occupants of large territories are penalized by decreased efficiency in communal mobbing. However, in small larids, too, (with small territories) communal mobbing fails to deter predators once they are too superior, too large, notably mammalian, or nocturnal (Burger 1979, Southern et al. 1982, 1985, Jehl & Chase 1987). Predatory larids prove to be bold, vigorous and purposeful attackers, with some individuals specializing in a gull chick diet, while neighbouring conspecifics feed on normal food items (e.g. Harris 1964, Kadlec & Drury 1968, Southern & Southern 1984). In the large mixed colony studied by Southern & Southern (1984), with several thousand pairs of Ring-billed Gulls and a few hundred Herring Gulls, only about 2% of Herring Gulls were responsible for killing and devouring about 10% of the Ring-billed Gull offspring. The smaller species appeared to lack effective defences for coping with this predation (Southern & Southern 1984).

The same superiority applies to cannibalistic gulls. In the study of Parsons (1971), cannibal Herring Gulls took 23% of a sample of 1 415 ringed chicks; just over half of these were eaten by only four cannibals.

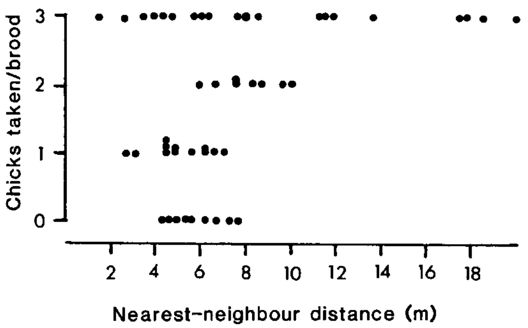

Fig. 5. The relationship of nearest-neighbour distance to the number of chicks/brood taken by predatory Herring Gulls. Each dot represent one three-chick brood. Nearest-neighbour distance did not differ between the groups (Kruskal-Wallis test, H = 4.077, df = 3, P = 0.25) because of the trendless distribution among the totally predated broods (the uppermost group).

Even though increased numbers of defenders taking part in communal mobbing may reduce predator success (e.g. Tinbergen 1952, Kruuk 1964, Patterson 1965, Fuchs 1977) it cannot wholly prevent the hunting of competent specialists. This was the situation at Söderskär where predation was one of the major causes of death among Lesser Black-back chicks even though only 2–4% of Herring Gulls were proven predators. These specialists commonly took all three chicks in a brood regardless of the size and the situation of the target territory (Fig. 5). They were mainly neighbouring Herring Gulls selecting any territory within their reach (sight?). The long-distance predators took mainly "stray" chicks, and were less capable of exploiting the whole brood.

As far as the long-distance predation is concerned this pattern of nest clumping fits the model of Hunt & Hunt (1976, "probability of chick losses lowered in smaller territories") However, no one feature of individual territories seems to give effective protection against predation by neighbouring Herring Gulls, i.e. "purposeful attackers". Neither nest clumping nor wide spacing lowered the predation pressure in territories where all the three chicks were taken by predators (Fig. 5).

In conclusion: despite being a relatively "large" gull with a relatively large territory size and, consequently, a poor potential for communal defence, the nominate race of the Lesser Black-backed Gull shows behavioural analogies to the smaller, inoffensive gulls: it shows no intraspecific predation and lacks effective protection against interspecific predation. Kilpi (1988a, 1989) considers communal mobbing in large gulls only apparent as the defenders in a colony are not engaged in mutual "helping" but are in fact defending only their own territories. Joining a mobbing flock allows for a synchronous return to the nest after disturbance, this preventing dangerous neighbours from preying on the clutch (Kilpi 1988a). In the inoffensive Lesser Black-backed Gull even this behaviour is poorly evolved, and an approaching avian predator has no difficulties in breaking through the modest "aerial defence".

Herring Gulls have invaded the whole Finnish coastal area in about 45 years (Kilpi 1988b). Up to the 50s and 60s the nominate race of the Lesser Black-backed Gull was the only numerous "large" gull in Finland (Bergman 1939, 1982). Apparently, offspring-defence against predatory gulls was not a necessity in the original situation. The evolutionary time for the development of a new anti-predator device might have been too short.

Acknowledgements. I thank Juhani Apunen, Pertti Muuronen, Markku Nygård and Karl Selin for field assistance, Mikael Kilpi for discussions on the draft, and Joanna Burger and an anonymous referee for comments on the manuscript.

Selostus: **Harmaalokin saalistuksen vaikutus nimirodun selkälokin poikastuottoon**

Vuosina 1977–93 Söderskärin tutkimusalueen selkälokit keskisellä Suomenlahdella vähenivät 11%:n vuosivauhtia (Kuva 2). Alhainen lentopoikastuotanto, keskimäärin 0.18/pari, ei riittänyt korvaamaan aikuiskuolevuutta, jota kiihdyttivät selittämättömät kannanromahdukset (20–40%) vuosina 1983, 1986, 1989 ja 1993.

Harmaalokin saalistus verotti poikasista aluksi vähintään 17% (poikasten renkaat löytyivät harmaalokkien saalisjätteistä; Taulukko 1). Saalistajien (2 paria tai vähintään toinen puolisoista) poistamisen jälkeen tutkimusyhdyskunnan poikastuotanto koheni merkitsevästi ja saalistettujen poikasten osuus pieneni 2 %:iin. Saalistus ei kuitenkaan kokonaan loppunut, sillä saalistajia tuli myös kauempaa lähisaaristosta; koko Söderskärin alueella näitä "kaukosaalistajia" liikkui jokaisessa selkälokkiyhdyskunnassa (Kuva 3). Vaikka harmaalokkikannan rajoitustoimissa pesintöjen määrä väheni 40 % neljässä vuodessa, saalistusta ei saatu kokonaan loppumaan. 20–50 % harmaalokeista yritti korvauspesintää, ja kanta tuotti piiloisilla pesinnöillään vuosittain keskimäärin 0.12 poikasta/pari. Lokinpoikasiin erikoistuneita saalistajia oli arviolta vain 2–4 % harmaalokkipareista. Näiden jäljittäminen oli kuitenkin työlästä ja poistaminen vielä vaikeampaa.

Johtopäätöksenä on, ettei umpimähkäinen, suurisuuntainenkaan harmaalokkien vähentäminen välttämättä poista saalistusta, ellei jokaista saalistajaa erikseen löydetä ja poisteta. Käytännössä tehtävä osoittautui mahdottomaksi Söderskärin oloissa. Muutamankin saalistajan jääminen kantaan johtaa poikastappioihin ja myös saalistuksen nopeaan yleistymiseen lokkien käyttäytymisessä. Saalistuksen tuottamat poikastappiot eivät kuitenkaan välttämättä ole kohtuuttomia, mikäli muut tappiotekijät pysyvät pieninä. Söderskärin selkälokeilla kuitenkin poikasten elinsairaudet (Kuva 4) ovat siinä määrin yleisiä (n. 70 % poikasista kuoli sairauksiin), ettei tuotanto tätä nykyä kestä harmaalokin saalistuksen tuottamaa ylimääräistä hävikkiä (≥ 20 % Kuvan 4 poikasista). Tämä kirjoitus ei kuitenkaan ole kannanotto yleisten lokkien rajoituskampanjoiden puolesta.

Nimirodun selkälokki on ilmeisen altis isojen lokkien poikassaalistukselle. Tutkimusyhdyskunnassa saalistukseen erikoistuneet harmaalokkiyksilöt sieppasivat pesyeen kaikki kolme selkälokin poikasta riippumatta pesätiheydestä (Kuva 5). Tämä kuvastanee emojen ilmapuolustuksen heikkoutta määrätietoisia saalistajia vastaan. Sitä vastoin "kaukosaalistajat" sieppasivat yleensä vain osan pesyeestä ja tämänkin yhdyskunnan harvemman asutuksen alueilta, mikä kuvastanee kaukosaalistuksen sattumanvaraisuutta.

Selkälokin reviirikoko ja pesyeen puolustus saattavat olla sopeutumia menneeseen aikaan, jolloin se itse oli Suomenlahden pohjoisrannikon ainoa runsaslukuinen koloniaalinen iso lokki, eikä tehokas puolustus yhdyskunnassa ollut välttämättömyys.

References

Bergman, G. 1939: Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. — Acta Zool. Fennica 23:1–134.

— 1965: Trutarnas konkurrensförhållanden, födobehov och relationer till andra skärgårdsfåglar. — Zoologiska Revy 7:58–77.

— 1982: Population dynamics, colony formation and competition in Larus argentatus, fuscus and marinus in the archipelago of Finland. — Ann. Zool. Fennici 19:143–164.

Bevanger, K. & Thingstad, P. G. 1990: Decrease in some Central Norwegian populations of the northern subspecies of the Lesser Black-backed Gull (Larus fuscus fuscus) and its possible causes. — Fauna Norwegian, Ser. C. Cinclus 13:19–32.

Brown, R. G. B. 1967: Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls Larus argentatus and L. fuscus. — Ibis 109:502–515.

Burger, J. 1974: Breeding adaptations of Franklin's Gull (Larus pipixcan) to a marsh habitat. — Anim. Behav. 22:521–567.

— 1979: Competition and predation: Herring Gulls versus Laughing Gulls. — Condor 81:269–277.

— 1981: Super territories: a comment. — Am. Nat. 118:578–580.

Burger, J. & Gochfeld, M. 1983: Behavioural responses to human intruders of Herring Gulls (Larus argentatus) and Great Black-backed Gulls (L. marinus) with varying exposure to human disturbance. — Behavioural Processes 8:327–344.

Butler, R. G. & Trivelpiece, W. 1981: Nest spacing, reproductive success, and behavior of the Great Black-backed Gull (Larus marinus). — Auk 98:99–107.

Cramp, S. (ed.) 1985: The Birds of the Western Palearctic. Vol. IV. — Oxford University Press.

Davis, J. W. F. & Dunn, E. K. 1976: Intraspecific predation and colonial breeding in Lesser Black-backed Gulls Larus fuscus. — Ibis 118:65–77.

Duffy, D. C. 1979: Human disturbance and breeding birds. — Auk 96:815–816.

Emlen, J. T. Jr. 1956: Juvenile mortality in a Ring-billed Gull colony. — Wilson Bull. 68:232–238.

Fetterolf, P. M. 1983: Effects of investigator activity on Ring-billed Gull behavior and reproductive performance. — Wilson Bull. 95:23–41.

Fordham, R. A. 1970: Mortality and population change of Dominican Gulls in Wellington, New Zealand. — J. Anim. Ecol. 39:13–27.

Fuchs, E. 1977: Predation and anti-predator behaviour in a mixed colony of terns Sterna sp. and Black-headed Gulls Larus ridibundus with special reference to the Sandwich Tern Sterna sandvicensis. — Ornis Scand. 8:17–32.

Götmark, F. 1982: Coloniality in five Larus gulls: a comparative study. — Ornis Scand. 13:211–224.

Hario, M. 1981: Impact of the Herring Gull on the breeding of the Lesser Black-backed Gull (In Finnish with English summary). — Lintumies 16:25–29.

— 1989: The decline of the nominate race of Lesser Black-backed Gull (Larus f. fuscus) in the eastern part of the Gulf of Finland (In Finnish with English summary). — Lintumies 24:204–212.

— 1990: Breeding failure and feeding conditions of Lesser Black-backed Gulls Larus f. fuscus in the Gulf of Finland. — Ornis Fennica 67:113–129.

Hario, M., Komu, R., Muuronen, P. & Selin, K. 1986: Population trends among archipelago birds in Söderskär bird sanctuary 1963–86 (In Finnish with English summary). — Suomen Riista 33:79–90.

Harris, M. P. 1964: Aspects of the breeding biology of the Gulls Larus argentatus, L. fuscus and L. marinus. — Ibis 106:432–456.

Haycock, K. A. & Threlfall, W. 1975: The breeding biology of the Herring Gull in Newfoundland. — Auk 92:678–697.

Hudson, A. 1982: Great Black-backed Gulls on Great Saltee Island, 1980. — Irish Birds 2:167–175.

Hunt, G. L. Jr. & Hunt, M. W. 1975: Reproductive ecology of the Western Gull: the importance of nest spacing. — Auk 92:270–279.

— 1976: Gull chick survival: the significance of growth rates, timing of breeding and territory size. — Ecology 57:62–75.

Jehl, J. R. Jr. & Chase, C. III. 1987: Foraging patterns and prey selection by avian predators: a comparative study in two colonies of California Gulls. — Studies in Avian Biology 10:91–101.

Kadlec, J. A. & Drury, W. H. Jr. 1968: Structure of the New England Herring Gull population. — Ecology 49:644–676.

Kadlec, J. A., Drury, W. H. Jr. & Onion, D. K. 1969: Growth and mortality of Herring Gull chicks. — Bird-Banding 40:222–233.

Kilpi, M. 1983: Population trends and selection of nest sites in Larus argentatus and L. fuscus on the Finnish coast. — Ornis Fennica 60:45–50.

— 1988a: Offspring-defence behaviour towards a human intruder in three species of gulls: Larus marinus, L. argentatus and L. canus. — Ornis Fennica 65:156–162.

— 1988b: Breeding and movements of the Herring Gull Larus argentatus in the northern Baltic: strategies for reproduction and survival of a successful species. — PhD Thesis, University of Helsinki.

— 1989: Solitary pairs of Great Black-backed Gulls Larus marinus prevent strangers from mobbing a predator model at their nest site. — Ornis Fennica 66:77–79.

Kostina, G. N. & Panov, E. N. 1982: Mortality of chicks and stability of personal bonds between chicks and parents in Larus ichtyaetus. — Zool. Zh. 61:1531–1542.

Kruuk, H. 1964: Predators and anti-predator behaviour of the Black-headed Gull. — Behaviour, suppl. 11:1–129.

Mousseau, P. 1984: A comparison of two methods to assess the breeding success of Ring-billed Gulls. — Journal of Field Ornithology 55:151–159.

Paludan, K. 1951: Contributions to the breeding biology of Larus argentatus and Larus fuscus. — Videnskabelige Meddelelser fra Dansk Naturhistorisk forening i Kobenhavn 114:1–128.

Parsons, J. 1971: Cannibalism in Herring Gulls. — British Birds 64:528–537.

— 1975: Asynchronous hatching and chick mortality in the Herring Gull Larus argentatus. — Ibis 117:517–520.

Patterson, I. J. 1965: Timing and spacing of broods in the Black-headed Gull Larus ridibundus. — Ibis 107:433–459.

Southern, L. K., Patton, S. R. & Southern, W. E. 1982: Nocturnal predation on Larus gulls. — Colonial Waterbirds 5:169–172.

Southern, W. E., Patton, S. R., Southern, L. K. & Hanners, L. A. 1985: Effects of nine years of fox predation on two species of breeding gulls. — Auk 102:827–833.

Southern, W. E. & Southern, M. D. 1984: Herring Gulls specialize as Ring-billed Gull predators. — Colonial Waterbirds 7:105–110.

Stenman, O., Komu, R. & Ermala, A. 1972: Finnish experience of poisoning Herring Gulls and Great Black-backed Gulls with chloralose (In Finnish with English summary). — Suomen Riista 24:107–116.

Strann, K.-B. & Vader, W. 1992: The nominate Lesser Black-backed Gull Larus f. fuscus, a gull with a tern-like feeding biology, and its recent decrease in northern Norway. — Ardea 80:133–142.

Tinbergen, N. 1952: On the significance of territory in the Herring Gull. — Ibis 94:158–159.