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Breeding failure and feeding conditions of Lesser Black-backed Gulls *Larus f. fuscus* in the Gulf of Finland

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A ten-year study of the breeding success of Lesser Black-backed Gulls in a mixed colony in the Gulf of Finland revealed a high rate of parental failure in years of low rates of provisioning for the chicks. The parents ate their own eggs at the rate of 16% per annum (range 0–52%), and on average 13% of the chicks (range 0–25%) remained unfed. No such anomalies were detected among Herring Gulls in the same colony.

Both gull species fed on the Baltic Herring, which occurred in 71.8% of the regurgitations of Lesser Black-backed chicks. The chicks' begging behaviour was normal, and the need to guard the nest from local Herring Gulls was not observed to restrict the foraging opportunities of the Lesser Black-backed adults.

The Lesser Black-backed parents were divided into three groups according to their chick-rearing result. The least effective group showed no response to the variation in the biomass of the spawning Herring stock in the Gulf of Finland. However, the occurrence of this group seemed to be connected with some unknown food-related factors. It is concluded that neglect of brood care is either a rough reaction to variation in feeding conditions, or the symptom of unknown harmful physiological changes.

1. Introduction

The long decline in the population of the nominate race of the Lesser Black-backed Gull *Larus f. fuscus* in Finland has evoked concern about the extent to which food is a limiting factor for the reproduction of this highly piscivorous gull (e.g. Bergman 1982, Hario 1985a). The abundance of the Sprat *Clupea sprattus* has decreased drastically in the Baltic Sea since the early 1970s, while the commercial catch of the Baltic Herring *C. harengus* has increased by 50% during the same period (Parmanne 1988, Parmanne & Sjöblom 1988). The situation may be similar to that in the Northeast Atlantic, where the fisheries' claimed overexploitation of diminishing fish stocks has coincided with the population decline and breeding failure of seabirds over vast areas (e.g. Lid 1981, Vader 1987, Barrett & Haug 1989, Monaghan et al. 1989, Avery & Green 1989). The remnants of the Norwegian population of the nominate race of the Lesser Black-backed Gull are also thought to suffer from poor feeding conditions (Bevanger & Thingstad 1990).

In the Gulf of Finland, the diminishing Lesser Black-backed Gull colonies produce 0.1–0.5 fledglings/pair (Hario 1985a, 1989). Most pairs fail to raise any young at all. Starvation of chicks amounts to 20%. The ultimate causes of the starvation and poor chick growth have remained uncertain.

In this paper, breeding parameters will be related to the variation in the quality and, to some extent, the quantity of food in the Gulf of Finland.

2. Material and methods

The study was conducted at the Söderskär Game Research Station in the outer archipelago of the Gulf of Finland, about 25 km southeast of Helsinki (Fig. 1). The study area is a bird sanctuary, consisting of 25 islets, all rich in seabirds, with gulleries and terneries of various sizes on every islet. The population trend of the Lesser Black-backed Gull has been monitored intensively from the early 1950s, mainly by nest counts.

From 1980 on, counts were made of fledglings/clutch over the whole sanctuary, and a special study of the breeding success was started in a mixed colony of Lesser Black-backed and Herring Gulls ("Main study colony" in Fig. 1). This colony is about the second to third largest of the Lesser Black-backed colonies at Söderskär (n = 6–9, numbers varying annually due to splintering and overall decline). Its number of fledglings per clutch has been about equal to that for the whole Söderskär area (annual mean 0.24 vs. 0.20 in 1980–89, range 0.04–0.77 vs. 0.08–0.45), and no evidence could be discerned of young/poor-quality individuals predominating in this colony. The age structure is not known, but the plumage characters of the colony members seem to fit the overall picture from the whole sanctuary: prospecting immatures are hardly ever present. Interchange of breeding birds with other Lesser Black-backed colonies in the Gulf of Finland seems improbable: the closest major colo-

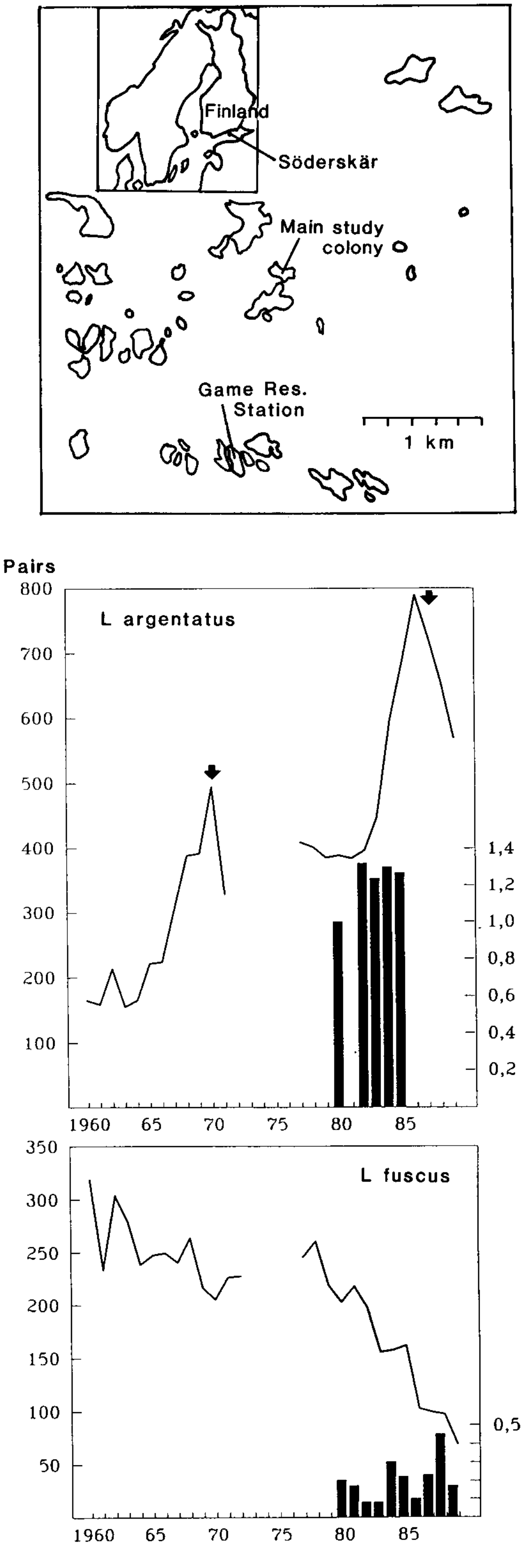

Fig. 1. Location and map of islands at the Söderskär bird sanctuary. The graphs give the population trends of Lesser Black-backed Gulls (*L. fuscus*) and Herring Gulls (*L. argentatus*) at the sanctuary in 1960–89 (no data for 1973–75). Bars indicate the mean numbers of fledglings per nest in different years (scale to the right). Arrows give the years of culling of Herring Gulls.

nies lie 100 km away in the east and these are declining at the same rate (see Hario 1989).

Every year, nests were marked and mapped as soon as they were located, and laying was surveyed on a nest-by-nest basis during visits at 1–2-day intervals. Eggs were marked (on the blunt end) in water-proof ink with their ordinal number in the clutch. In order to check the mutual hatching sequence, each chick in a clutch was marked by injecting a small portion of commercial dye into the pipping egg. The dyed chicks (a slight tinge of red or green in the ventral down) were ringed within 1–3 days of hatching. From 1981 on, inclusive, their body weight was monitored during daily visits, weather permitting. Whenever a chick was found, it was weighed to the nearest 0.5 g with a spring balance. When older, the chicks hid well among vegetation, and it was not possible to find every chick every day.

The vitality of the chicks was assessed by examining their reaction to sign stimuli of the gull parent's bill, following the description given by Tinbergen (1953). The number of pecks/30 sec. made by the chick on the model (see the photograph in Hario 1985a) were counted on three occasions during the first day of the chick's life. The individual rate of response was recorded as the mean number of pecks made by a chick in three tests. The experiments were done in 1983 and 1988.

Weight curves were fitted by eye; no equations for smoothing were used because of the scarcity of material in older age groups and lack of asymptotic weights. These shortcomings result from the fact that the young were not nourished normally in most of the study years.

Data on the composition of the diets of Lesser Black-backed Gulls were collected by examining pellets found at nest sites and spontaneous regurgitations of chicks when being handled. Details of sample sizes are given in the relevant tables and text sections.

The frequency with which the young were fed and guarded was studied by direct observation from a blind during the first 7 days of a chick's life. Only 3-chick broods were involved. A total of 146 nest-hours of observation was made on 14 nests of Lesser Black-backed Gulls and on 3 nests of Herring Gulls during the 1984–87 breeding seasons.

The daily rhythm of foraging activity was studied by monitoring the numbers of attending adults in the colony throughout the chick-rearing periods of 1984–89. The numbers of gulls flying away from the colony and returning to it were counted during 2–12-h watches (a total of 198 hours) in 1987–89. These movements were observed from a blind on the highest vantage point of the sanctuary, from which the flight directions could readily be seen.

The data on the weather conditions are based on daily records from the Game Research Station. The assessments of the clupeid stocks were derived directly from the data in the ICES reports, submitted by the Fisheries Division of the Finnish Game and Fisheries Research Institute.

3. Results

3.1. Population trends and overall breeding success

The decline of the Lesser Black-backed Gull population at Söderskär averaged 2% per annum during 1961–72 and 10% per annum during 1978–89 (Fig. 1). The latter rate is affected by sudden drops of 23%, 39% and 33% in 1983, 1986 and 1989, respectively (due to elevated adult mortality outside the breeding season, Hario 1989). The reasons for the decline in the 1960s are not known.

The fledging rates for the whole Söderskär area during 1980–89 varied between 0.08 and 0.45 (annual means) averaging 0.20 fledglings/clutch (SD = 0.11). This can be compared with the mean fledging rate of Herring Gulls in the same area in 1980–85: 1.23 (SD = 0.13; for details, see Hario 1985a).

3.2. Egg losses

In the study colony, the annual egg losses varied between 11% and 68%, averaging 36% during 1980–89 (Table 1). The high rate of egg-eating (mean 16%) is striking and stands in strict contrast to what was found among the Herring Gulls in the same colony during 1980–84 (4 eggs out of 257 or 1.6%, Hario 1985a). In nearly every

Table 1. Certain breeding parameters of Lesser Black-backed Gulls in the main study colony in 1980–89.

	No. of nests[1]	No. of eggs	Eggs eaten at nest %[2]	Total egg losses %	Chick starvation %[3]	Total chick losses %	Chicks' weight gain g[4]	Fledglings % of chicks	Fledglings % of eggs
1980	25	65	20.0	50.8	12.5	96.9	..	3.1	1.5
1981	31	83	19.3	41.0	24.5	95.9	60	4.1	2.4
1982	22	60	20.0	40.0	25.0	97.2	60	2.8	1.7
1983	15	41	7.3	12.2	11.1	97.2	65	2.8	2.4
1984	13	38	0	10.5	0	70.6	100	29.4	26.3
1985	21	57	3.8	21.1	6.7	82.2	105	17.8	14.0
1986	17	37	10.8	40.5	4.5	95.5	95	4.5	2.7
1987	13	26	23.0	46.2	13.3	80.0	55	20.0	11.5
1988	22	56	10.7	30.4	2.6	60.5	100	39.5	26.8
1989	11	25	52.0	68.0	25.0	87.5	50	12.5	4.0

[1] Corresponds to colony size. Renests excluded (0–3 cases annually, producing no fledglings).
[2] All the eggs/clutch eaten plus nest demolished.
[3] Starved chicks as % of chicks hatched.
[4] Weight on the 7th day of life minus hatching weight. Data from the curves in Fig. 7.

case, the whole clutch were eaten, and the nest was torn down (designated "eaten at nest" in Table 1). This systematic extermination was done by the parents themselves, as was verified in two instances by direct observation from the blind: apparently unalarmed, the incubating bird stood up and with active pecking broke the shell and partially consumed the contents. The egg shells were not removed; instead the bird demolished the nest and walked or flew away. No renesting attempts occurred in these cases.

Of the clutches that were entirely destroyed together with the nest, 17 (59%) belonged to late layers (= last laying third of the study colony) and 9 (31%) to median layers. Only 3 (10%) stemmed from early breedings (= first laying third); these were from the years 1988–89 when the phenomenon was becoming increasingly frequent (see Table 1). The incubation stage at which the eggs were eaten varied from 4 days to pipped eggs, averaging 10 days (±6, SD) for late layers and 12 days (±7) for median layers.

3.3. Chick losses

The annual chick losses were heavy among Lesser Black-backed Gulls, varying between 61% and 97% and averaging 86% (Table 1). The main causes were chick disappearance, predation by Herring Gulls, and starvation. The two first factors will be dealt with elsewhere (Hario in prep.).

Table 2. Comparison of chick losses of Lesser Black-backed Gulls and Herring Gulls in the main study colony in 1980–83 (percentage of totals in brackets). Fisher's exact test has been used. Data from Hario (1985a).

	Lesser Black-backed			Herring Gull	
Disappeared	88	(60)	NS	93	(68)
Starved at nest	29	(20)	P = 0.0001	7	(5)
Taken by predator	25	(17)	NS	20	(15)
Found dead, unknown causes	5	(3)	P = 0.004	17	(12)
Total losses	147	(100)		137	(100)

Again, the high frequency of starvation differed significantly from what was found among the local Herring Gulls (Table 2). Starving chicks lost weight from the very start and died in the nest within a few days (Fig. 2). Their digestive tract was empty. In contrast, those chicks that were later preyed upon by Herring Gulls showed the best growth rates (Fig. 2). Although the Herring Gull adults also preyed on chicks of their own species, there was no such difference in growth rates between the chicks preyed on and those not

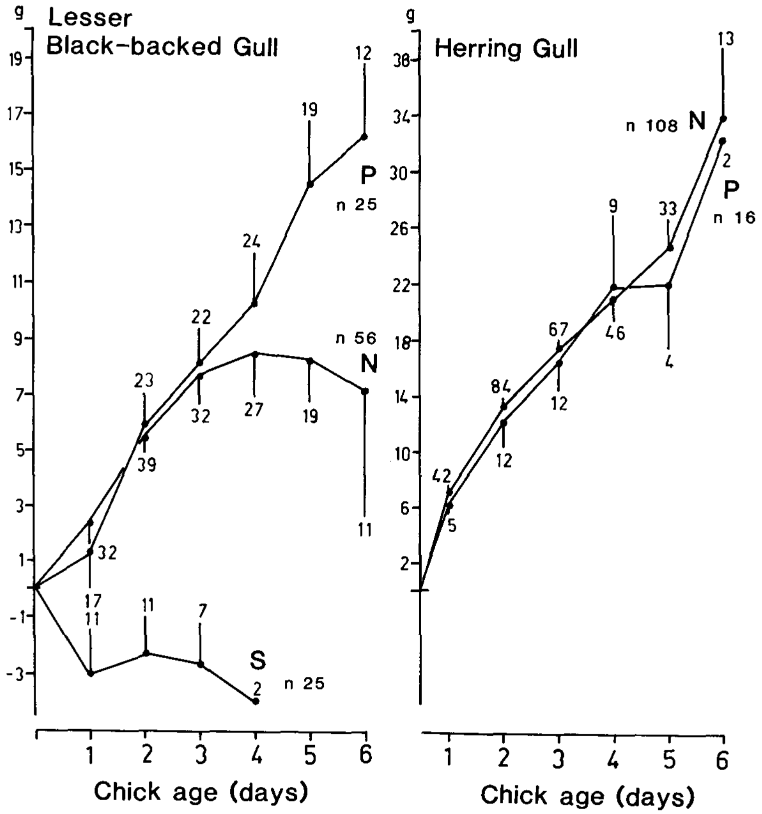

Fig. 2. Mean daily weight gain (+ or −SE) of Lesser Black-backed and Herring Gull chicks in 1981–83. P = chicks taken later by predators, N = chicks not taken by predators, S = starved chicks. Figures above/below SE denote the sample size in each age cohort; n = total number of individuals. Day of hatching = 0.

preyed on (Fig. 2). This implies that all the Herring Gull chicks were equally well nourished and equally prone to predation (equally mobile and lively?). Predation never affected starving Lesser Black-backed Gull chicks dying in their nests and not moving outside their territory.

A common observation in gull studies is that the last-hatched chick in a clutch is at a disadvantage compared with its siblings; it shows both higher mortality and a slower growth rate (e.g. Lundberg & Väisänen 1979, Viksne & Janaus 1980, Hébert & Barclay 1986, Pierotti & Bellrose 1986, Reid 1987 and references therein). The growth data in Fig. 2 are biased against these last-hatched chicks in that only 8% of the chicks taken as prey were last-hatched chicks whereas in the group not taken by predators they make up 29% (Fisher's exact test, P = 0.03). When their data are removed from the material, however, the same difference in growth patterns still emerges (Fig. 3). The starved group in Fig. 2 consists of whole broods, so a division according to hatching order is not meaningful.

3.4. Begging behaviour of chicks

The slow growth and high starvation frequency of the Lesser Black-backed chicks can be interpreted to result from either poor parental care or diminished efficiency of the chicks' begging behaviour (see Tinbergen 1953). Yet, compared with the Herring Gull chicks, all the newly hatched Lesser Black-backed chicks gave an equally good response to the sign stimuli of the gull parent's bill (Table 3). This suggests that the reasons for starvation lie in inefficient parental care, not in the chicks themselves. Their innate begging behaviour should have released feeding behaviour in the adults. Yet, nearly 20% of the chicks re-

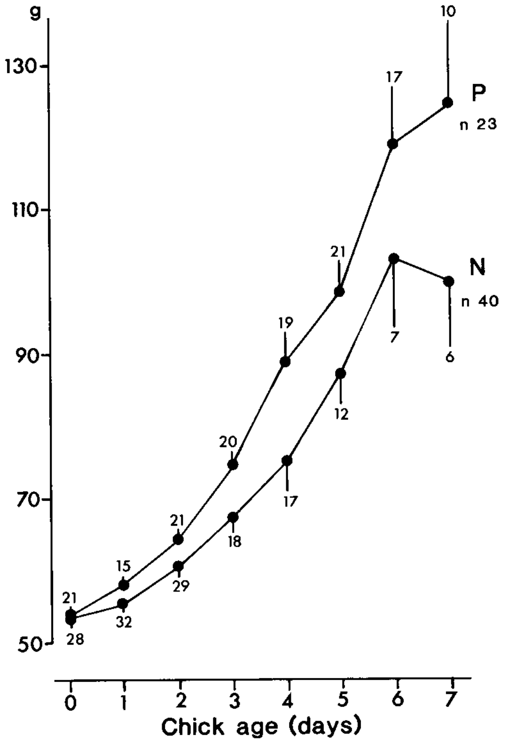

Fig. 3. Same material as in Fig. 2 for Lesser Black-backed Gull chicks taken (P) and not taken (N) by predators, but with the last-hatched chicks/clutch excluded (see text).

Table 3. Chick reaction to gull parent's bill (test model from Tinbergen 1953). Mean number of pecks/30 sec.±SD. Number of individuals in brackets. Between-cohorts testing not meaningful.

	Lesser Black-backed	Herring Gull
Chicks disappeared before the age of 7 days	15.2 ± 4.6 (19)	12.9 ± 3.5 (12)
Chicks known to have survived to the age of 7 days	14.4 ± 4.4 (20)	7.0 ± 5.3 (15)
Chicks starved at nest	10.4 ± 3.4 (10)	

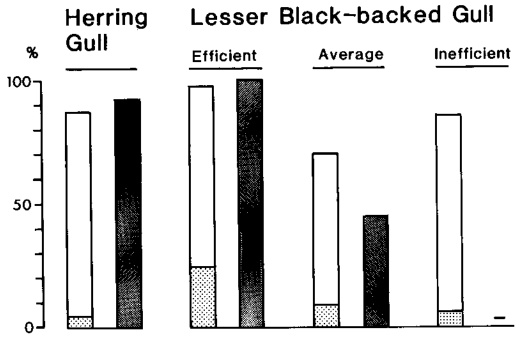

Fig. 4. Nest attendance (percentage of nest-hours) of one parent (white portions of columns) and both parents (dotted portions of columns) in Herring Gull and Lesser Black-backed Gull nests, and percentage proportion of feedings in which the food sufficed for all three chicks in a brood (dark columns). "Efficient" = pairs that raised all their chicks to the age of 7 days, "average" = pairs that raised ≥1 chick to the age of 7 days, "inefficient" = pairs that raised no chicks. Sample sizes: Herring Gulls = 3 pairs, 17 feedings, 34 nest-hours; Lesser Black-backed Gulls: "efficient" = 7, 21, 66; "average" = 3, 5, 16; "inefficient" = 4, 0, 30.

mained unfed in 1980–83, the corresponding figure for Herring Gulls being only 3% ($\chi^2 = 13.69$, df = 1, $P < 0.001$).

3.5. Time budgets of the adults

In order to find the reasons for this apparently inadequate parental behaviour, the following hypotheses were examined:

1) The parents were 'stressed' by the presence of Herring Gulls in the mixed colonies and had to allocate all the time to chick guarding, thus being unable to set off on feeding trips.
2) Some of the adults were simply unable to find food.
3) Some internal factor prevented the parent birds from making an adequate transition from brooding to chick feeding.

To test the validity of the first hypothesis, the time budgets of the inefficient parents were compared with those of the efficient parents and with efficient Herring Gull parents (Fig. 4). It was hypothesized that if the inefficient parents were stressed by the presence of the neighbouring Herring Gulls, their time division between nest attendance (guarding chicks) and absence from the nest (foraging trips) would differ from that of the efficient parents. However, the inefficient parents showed about the same sharing pattern for attendance duty as the efficient parents (and the Herring Gull parents): only one parent attended the nest at a time and the presence of both parents coincided with the short moments of nest relief (5.8% of the time monitored; 4% in Herring Gulls, 8.4% in "average" parents, 24.5% in efficient parents, see explanations for Fig. 4). Hence, the division of labour indicates that one of the inefficient parents was almost always "free" to go on foraging trips (off duty). The presence of Herring Gulls did not prevent them from taking off. Despite this, the returning gulls never fed their chicks (Fig. 4).

It is noteworthy that the intervals during which the chicks were left unguarded (both parents absent) were longest for the "average" parents (= those which were able to feed only some but not all of their chicks): 30% of the time recorded against 3% in efficient parents, 14% in inefficient parents and 14% in Herring Gulls ($P < 0.001$ for all comparisons, χ^2-test). This implies that "average" parents had to work harder to provide the food, even at the cost of reduced safeguarding. Even so, their foraging success remained low: in only 45% of the feedings did the food suffice for all three chicks, so that food appeared to be scarce for them but not for the efficient parents.

3.6. Diet of chicks

Not many food castings could be established during the almost daily searches made on a nest-by-nest basis in two Lesser Black-backed colonies during the chick rearing periods of 1981 and 1984–89 (Table 4). Intact food (rejected by chicks, see Annett & Pierotti 1989) was only seldom encountered on the nest sites, which indicated that there was no surplus food for chicks or adults. Pellets found on nest sites made up 55% of the total castings, and spontaneous regurgitations by chicks 45%.

In chick regurgitations, the frequency of Clupeoids was highest among the food items, totalling 71.8%. The material is too scanty to allow a meaningful comparison between years, but in nearly every year studied (exception: 1981), Clupeoids (Herring/Sprat) had the highest frequency among the food items found in regurgitations (range 50–86%).

There are great differences in the residence times of soft parts of prey items in the stomach of seabirds, some persisting longer than others (for some extremes, see Furness et al. 1984). Pellets left at nest sites (mainly gizzard contents) are probably biased against soft-bodied prey (e.g. Irons 1987), whereas the spontaneous regurgitations by chicks (crop contents) may adequately represent the fresh food, i.e. the recent meal.

This may be the reason for the significant difference in Clupeoid frequencies between pellets and regurgitations (Table 4). In the pellets, Clupeoids were apparently too eroded for macroscopic examination. Herring eggs were readily detectable in most of the regurgitations but never in the pellets. In contrast, large-boned fish and Isopoda (notably *Saduria entomon*) occurred significantly more in pellets than in chick regurgitations. Insects seem to be a fairly important food

Table 4. Diets of Lesser Black-backed Gulls as indicated by presence (% occurrence) of different items in pellets (n = 48) and chick regurgitations (n = 39) collected in two colonies in 1981 and 1984–89 (materials combined). n = no. of castings containing the food item, % = % occurrence of the castings. Fisher's exact test has been used.

Food item	Pellets		Regurgitations		
	n	%	n	%	
Clupeoids	4	8.3	28	71.8	P < 0.001
Other fish[1]	12	25.0	2	5.1	P = 0.011
Insects[2]	22	45.8	13	33.3	P = 0.168
Saduria	12	25.0	3	7.7	P = 0.030
Plant matter[3]	5	10.4	11	28.2	P = 0.032
Garbage[4]	6	12.5	7	17.9	P = 0.340
Waste[5]	3	6.3	7	17.9	P = 0.086
Other items[6]	5	10.4	–		P = 0.058

[1] predominantly cyprinoids and cod

[2] mainly wasps, ants, beetles, dragonflies, ladybugs

[3] grass, moss, berries

[4] edible foodstuffs (chicken, pork, bread, etc.)

[5] non-edible stuff (small stones, piece of glass, plastic, etc.)

[6] small passerines, microtines, egg shells, etc.

item for Lesser Black-backed Gulls, as judged from the high frequencies in both pellets and regurgitations. Garbage was of minor importance.

Most of the pellets were probably left by adult birds. Judged from the regurgitations, the main food presented to Lesser Black-backed chicks was Herring/Sprat. Spawning Herring was also present in 63% of the 67 gizzard and crop contents of Herring Gull chicks from the surrounding colonies in the same study years. Garbage amounted to 15%, which is a rather low figure (cf. e.g. Lemmetyinen 1963, Andersson 1970, Spaans 1971, Götmark 1984 and references therein).

3.7. Feeding flights

The variation in the numbers of adult Lesser Black-backed Gulls leaving the colony and returning to it is shown in Fig. 5. The overall movement pattern fits the pattern of colony attendance. The arrivals were most frequent early in the morning, the departures increased towards the evening. During most of the day, adults were present at the colony, whereas the numbers were lowest at night. This indicates that night is the most active foraging time for Lesser Black-backed Gulls in the Gulf of Finland. As the nights at the latitude of the Finnish south coast are light throughout the birds' breeding season, nocturnal feeding apparently poses no problems to gulls. Overnight or early morning fishing has also been noted among Kittiwakes *Rissa tridactyla* in Scotland (Galbraith 1983).

There was a marked difference in flight directions between Lesser Black-backed Gulls and Herring Gulls. The former almost always flew southeast to the open sea, whereas the latter also flew northwards to the mainland (Fig. 6).

These spatial and temporal patterns can be attributed to the occurrence of the Baltic Herring off the Finnish coast. This fish has spawning areas dispersed throughout the archipelago zones. Spawning begins in early May in the inner zones and reaches the outer skerries (ridges and shallow-water seabeds) by July (e.g. Oulasvirta et al. 1985). The Lesser Black-backed Gull is a highly piscivorous gull (e.g. Lemmetyinen 1963, Goethe 1975, Götmark 1984). Its plunge-diving ability is considered more "advanced" than that of the more robust Herring Gull (Goethe 1975, Bergman 1982). Its fishing manoeuvres and nocturnal foraging habits can be regarded as adaptations to the nightly vertical movements of Herring schools,

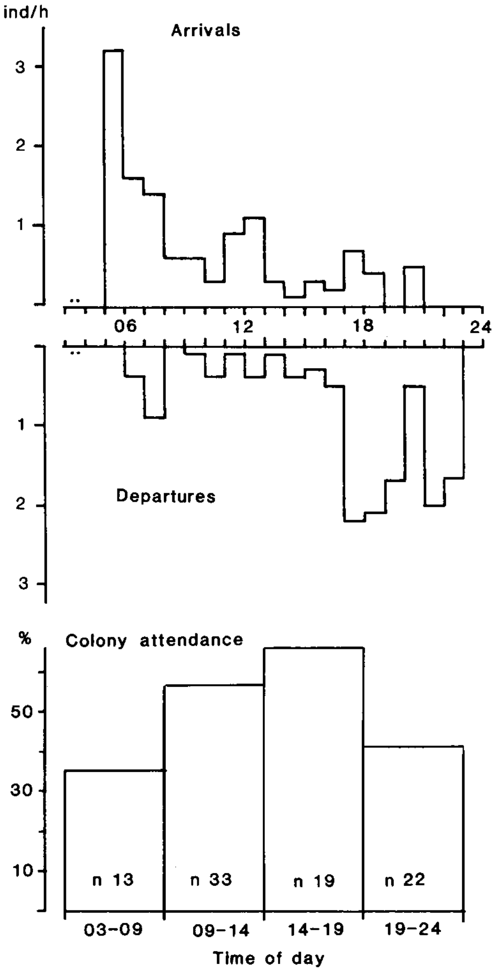

Fig. 5. Daily rhythm in foraging flights of Lesser Black-backed Gulls; individuals/hour arriving at and departing from Söderskär gulleries during the chick-rearing periods of 1987–89 (combined). The lower histogram gives the diurnal variation in colony attendance: percentage of adults (of the expected numbers derived from nest counts) present at the colony at different times of the day during the chick-rearing periods of 1984–89 (combined, n = no. of counts). Chick-rearing period defined as the period between 80% hatching and the first young fledging.

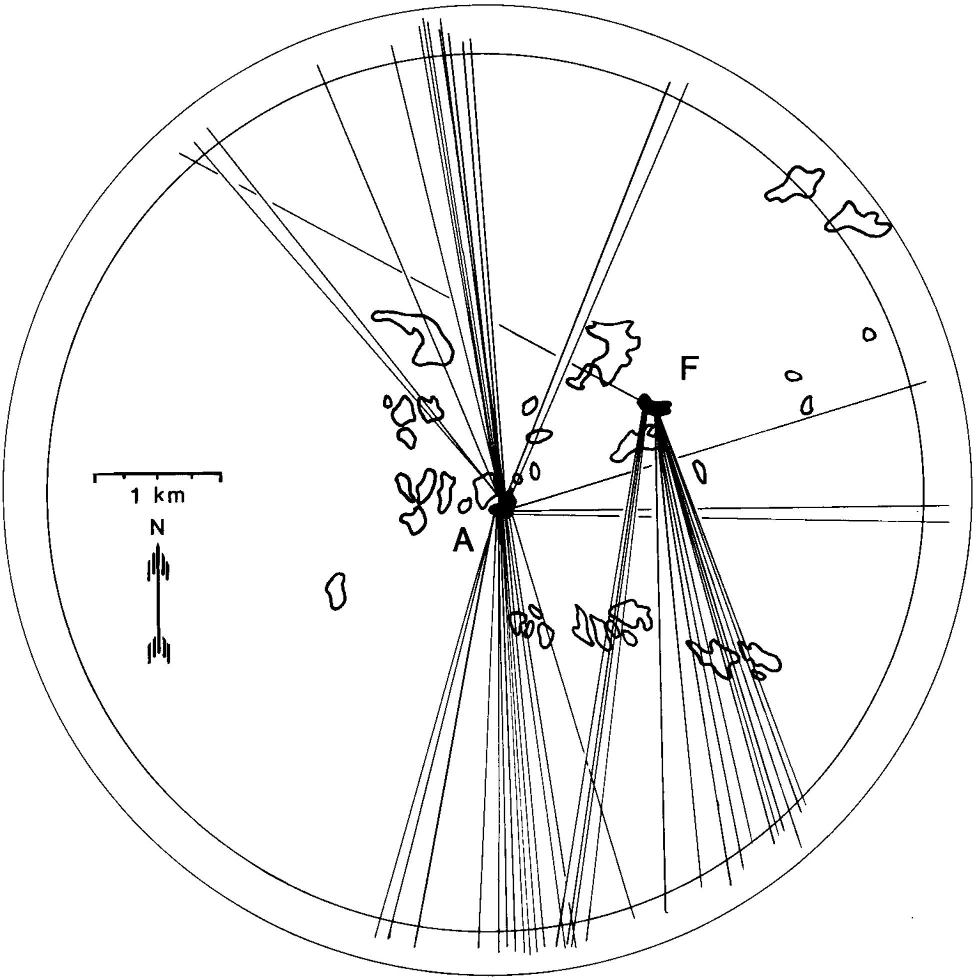

Fig. 6. Flight directions of departing Lesser Black-backed Gulls (colony F) and Herring Gulls (colony A) during the chick-rearing period in 1989; various dates, total observation time 30 h. Each line denotes one bird; the circle gives the distance at which the birds disappeared from sight (4–5 km). In the south, there is open sea, and in the north, the mainland.

which move towards the surface at dusk and towards the seabed at dawn (e.g. Blaxter & Hunter 1982, Oulasvirta et al. 1985; for larvae, see Sjöblom & Parmanne 1978). This well-known phenomenon is utilized by the trawling fishery in the Baltic waters in summer. To what extent the food of gulls stems from trawls (or from trapnets) is unknown. Bergman (1982) considers that the ability of the Lesser Black-backed Gull to catch free-swimming fish is limited (in the daytime?). The attraction to trawlers needs to be tested, as it varies widely among seabirds (Ryan & Moloney 1988).

The exact location of the gulls' feeding areas is unknown. They fly beyond the sight of an observer, disappearing over the sea. The arrivals show a similar flight direction distribution to that of the departures, with 85% of the Lesser Black-backed Gulls (n = 93) coming from the S-SSE and 12% from the SW. The rest came from easterly directions and only one from the north. The arrivals of Herring Gulls were not recorded.

3.8. Access to feeding

From the evidence presented above, it seems that the inefficient parents had the same opportunities to forage successfully as the efficient parents: their time-partitioning between nest attendance and off-duty was practically the same as that of the efficient parents, and they probably also used the same foraging areas, as judged from the uniform flight direction distribution. The bulk of the Lesser Black-backed population raised their chicks on Baltic Herring. It is hard to believe that the birds were simply unable to find any food during the 2–4 days for which a starving chick stays alive (starvation judged from continuous weight loss and subsequent empty alimentary tract). The begging behaviour of the chicks was normal. Therefore it seems reasonable to conclude that the inefficient parents simply "neglected" their feeding duty for some reason.

3.9. Evidence of food-related factors

The starved chicks (Fig. 2) were discarded from the growth rate data in Fig. 7. Despite this, the growth rates (= weight gain by the 7th day of life) of the remaining chicks correlated significantly with the proportion of starved chicks in the yearly cohorts (= chick starvation % in Table 1; r_s = –0.820, P = 0.020): the more starving chicks there were, the less the surviving chicks weighed. A similar correlation applies to the egg-eating frequency (r_s = –0.883, P = 0.013), which, in turn, also correlates with the chick starvation frequency (r_s = 0.803, P = 0.030). This close relationship between these three variables during the 9-year study period (no weight data were available in 1980) seems to call for a joint food-related explanation.

4. Discussion

4.1. Gulls eating own eggs

The proximate reasons for the very aberrant behaviour of the gulls eating their own eggs remained obscure. The visits to the colony were always kept to a minimum during the peak incubation period. However, as most egg-eatings occurred among late breeders, a certain amount of disturbance occurred during the concurrently increasing research on hatchlings. The possibility that the research activity in the colony was sufficiently disturbing to cause the aberrant behaviour is excluded by the large yearly differences in egg-eating frequency: from 0% to 52% of eggs laid (Table 1). There was no significant correlation between the egg-eating frequency and the annual synchrony in breeding (SD of days of laying initiation; r_s = 0.319), which rules out the possibility of the years with a longer laying span (and, consequently, more visits) having heavier stress than the more synchronous years.

Nest attendance is close to 100% during most of the incubation period (own obs.). However, interruptions of guarding may occur in less successful pairs showing unequal time-partitioning in clutch care activities between the partners, as was shown for Herring Gulls by Morris (1987). Tardiness in nest relief of the less active partner will lead either to prolonged solitary incubation by the more "faithful" partner, or to more frequent absenteeism of both partners.

In the latter case, the clutch will be exposed to partial or total predation. In the former case, the heavily committed partner might experience simultaneous drives to incubate and to leave the nest, as was suggested by Chardine & Morris (1983): the resulting displacement activity reported in two cases of Herring Gull breedings was egg-eating. This seems to fit the situations found among the Lesser Black-backed Gulls in the present study, as well. Although this behaviour, as a displacement activity, represents a rather "rough" reaction, it can be interpreted in the context of the food situation. The years of high egg-eating frequency were also years of slow chick growth and a high degree of chick starvation (see later). The possible prolonged absence of the less active partner may reflect food shortage, i.e. increasing effort required for food searching and, consequently, increasing time spent away from the nest. However, there is no quantitative evidence to support this assumption since no records of birds' time budgets were kept during the incubation period.

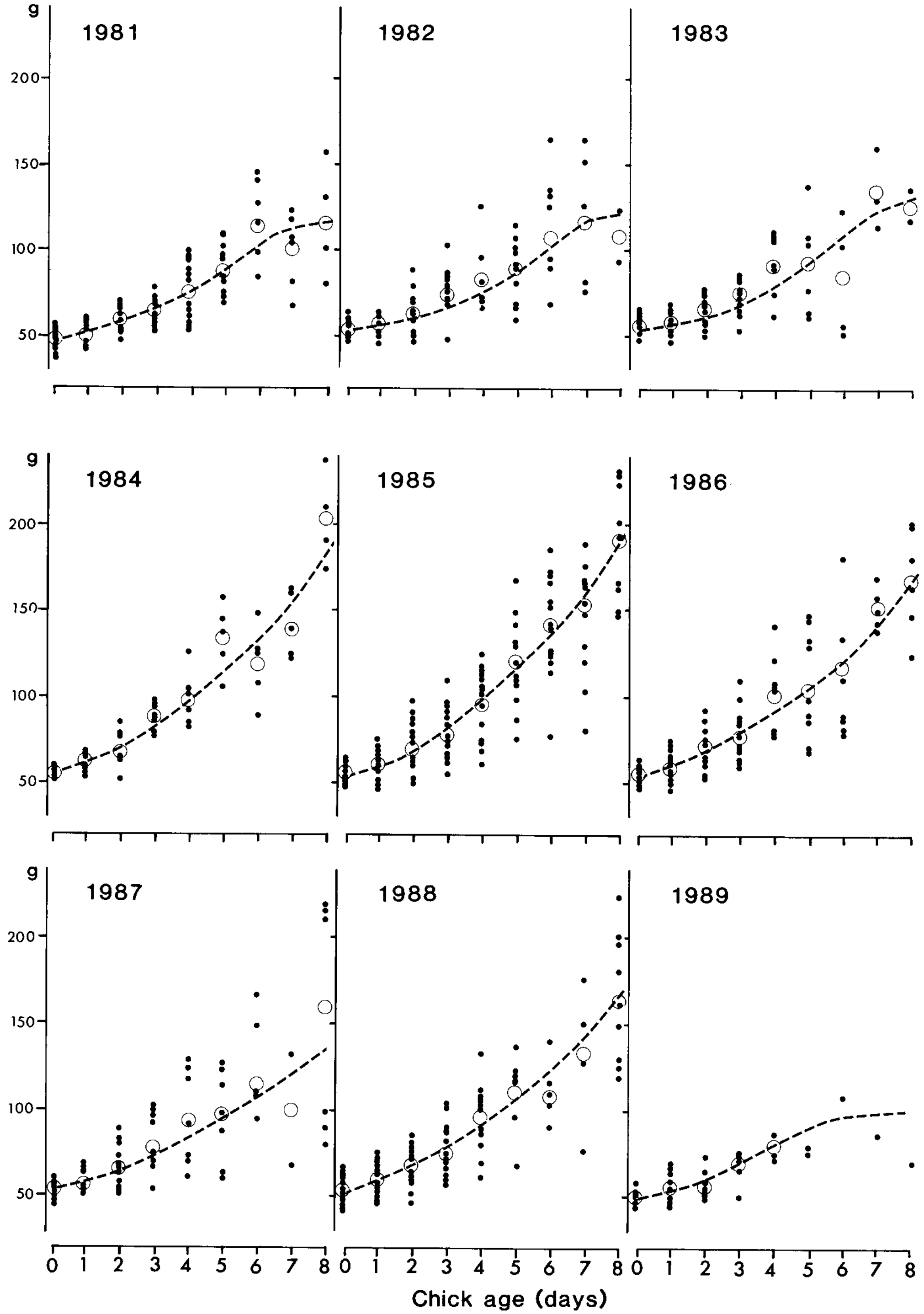

Fig. 7. Body weight of Lesser Black-backed chicks in 1981–89. Individual weights dotted, mean cohort weights marked with open circle, curves fitted by eye.

Widowed birds could be expected to exhibit the same response. However, in the studies conducted so far, the reactions have varied from successful re-pairing and uninterrupted incubation (Pierotti 1980) to female-female pairing and supernormal clutches (Conover 1984a, Conover & Hunt 1984) and to nest desertion and egg predation (Conover 1984b, Transue & Burger 1989).

4.2. "Average" parents

In the years 1981–83, 1987 and 1989, the overall growth rates of the chicks remained low, indicating nutritional deficits compared with better-quality years 1984–86 and 1988 (Fig. 7). In their paper on terns, Safina et al. (1988) suggested that hunger may intensify the conflict between the motivations for brooding and foraging; this conflict results in a higher rate of chick starvation in years when food is scarce. There are many examples of prey limitation lowering the reproductive performance of seabirds (e.g. Barrett & Runde 1980, Galbraith 1983, Brown & Nettleship 1984, Furness 1984, Barrett et al. 1987, Safina & Burger 1985, 1988, Safina et al. 1988, Monaghan et al. 1989). This happens either directly by chick starvation or indirectly by the foraging partners working harder at the expense of protection of the chicks, thereby increasing their vulnerability to predation. Commonly, both alternatives are involved, as in the case of "average" parents in this study. The crucial difference between them and inefficient parents was that they at least "had a try", so that their chicks showed a more "real" response to the between-year variation in the food situation, which, in fact, seemed to be considerable in 1981–89 (Fig. 7).

4.3. The effect of weather on food acquisition

No significant relationship was found between the yearly growth rate variation and the estimated biomasses of the spawning stock of the Baltic Herring in the Gulf of Finland (the latter derived from Anon. 1989) ($r_s = 0.325$, NS). For the egg-eating frequency and the frequency of chick starvation this correlation is even weaker (0.317 and –0.176).

For plunge-diving seabirds, prey availability may be modified by weather factors: hard wind and rain may alter the detectability and catchability of prey fishes (described for terns by Lemmetyinen 1972 and Dunn 1975). In the Gulf of Finland, the weather is seldom detrimental to feeding gulls, e.g. fog is hardly ever continuous for longer than 1 day (a 13-day fog in Canada lowered parental foraging in Herring Gulls, Hébert 1987), and hard winds are less frequent during the growth period of chicks in June than later in the summer (own obs.). Comparison between years showed that the first-week chicks tended to grow slower when the proportion of windy days was high ($r_s = -0.494$, NS), when there was much rain ($r_s = -0.603$, NS) and when the mean temperature during their growth period was low ($r_s = 0.470$, NS), but none of the weather parameters had as strong an effect on starvation frequency and egg-eating frequency (correlation coefficients varying between 0.006 and 0.322). This implies that the growth was modified by energetic stress (heat loss) during adverse weather rather than by food shortage.

4.4. Do castings reflect the prey situation?

It would be tempting to relate the numbers of castings to the above-mentioned parameters, but the numbers were always very low, reflecting the number of "live" nests rather than the variation in food abundance for chicks. Hence, the numbers were probably affected more by indirect factors (notably Herring Gull predation, reducing the number of live nests) than food availability or catchability.

Furthermore, apart from the extreme years, the prey composition in castings did not reveal significant differences in food preferences between "good" and "bad" years. When the food material was arranged according to annual cohorts (1984–86 and 1988 being years of "good" chick growth, and 1981, 1987 and 1989 being years of "bad" growth, see Fig. 7), there was no difference in the proportion of Clupeoids in chick regurgitations (Fisher's exact test, P = 0.261). This is most probably due to the fact that food samples were more readily obtained from the best-nourished chicks (full-fed) than from chicks

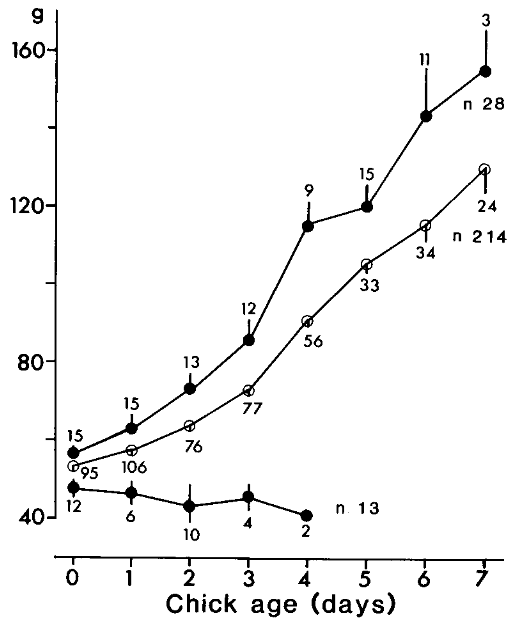

Fig. 8. Body weight of Lesser Black-backed chicks that regurgitated when being handled (filled circles) and those that did not (open circles). The fledging rate of the former group was 0.47 and of the latter group 0.21 ($\chi^2 = 8.51$, $P = 0.003$). Starved chicks (lowest curve) were excluded from the comparison. Data from two colonies in 1984–89. n = number of individuals.

receiving an average food supply or chicks that were fed at long intervals (Fig. 8). The regurgitating chicks were probably the offspring of the efficient parents, and these have no difficulties in preying on Clupeoids in most of the years. Only in 1981, when the spawning Herring stock biomass in the Gulf of Finland was the lowest for the period 1970–89 (Anon. 1989), was there a significant difference both in diet composition and in chick growth compared with the best growth year 1985 (Fig. 9).

Hence, the casting composition reflects only minor changes in the diet of efficient feeders, differences being marked only in extreme years.

The response of seabirds to food shortage varies widely; some species can alter their foraging ranges or diets, some are not equally flexible (for reviews see Furness 1984a, b; Brown & Nettleship 1984). The nominate race of the Lesser Black-backed Gull has several alternative food sources (see Table 4, Goethe 1975) and is therefore not entirely dependent on a single source, though there is apparently a threshold in Clupeoid abundance below which the species suffers from a food shortage in the Gulf of Finland. Ultimately, this may be connected with the high energetic value of Clupeoids (e.g. Furness & Barrett 1985, Barrett et al. 1987) compared with the alternative food items (insects, garbage etc., for ants, see Hario 1985b).

The spawning stock biomass of the Baltic Herring has approximately doubled in the Gulf of Finland (Soviet side included) during the 1980s (Anon. 1989). Against this background the poor chick growth, the high egg-eating frequency and the high starvation rate in 1989 appear enigmatic. Clearly, there must be other factors responsible for the inefficient parental behaviour among Lesser Black-backed Gulls than just the size of the preferred prey stock.

To sum up: the variation in feeding conditions most probably explains the shortcomings in feeding efficiency of the "average" parents. For efficient parents the effect of this factor is discernible only in extreme years (other contributory factors being the low energetic value of alternative food and adverse weather?). Furthermore, this factor seems to trigger the occurrence of inefficient parents in most of the years, but not in all (e.g. 1989).

4.5. Need for an alternative explanation

What is the cause of the occurrence of inefficient parents who never fed their chicks?

The percentage occurrence of inefficient parents and "egg-eating" parents in the main study colony correlates significantly with the yearly variation in the remaining chicks' growth rates ($r_s = -0.916$, $P = 0.009$), i.e. the poorer the feeding situation the higher the frequency of parental failure. However, parental failure did not correlate with the annual variation in the population size ($r_s = 0.122$, $P = 0.715$), i.e. there were not more failed parents when the adult population increased or fewer when it decreased. This indicates that the inefficient parents were actually "permanent" members of the colony, changing their response to the feeding conditions in differ-

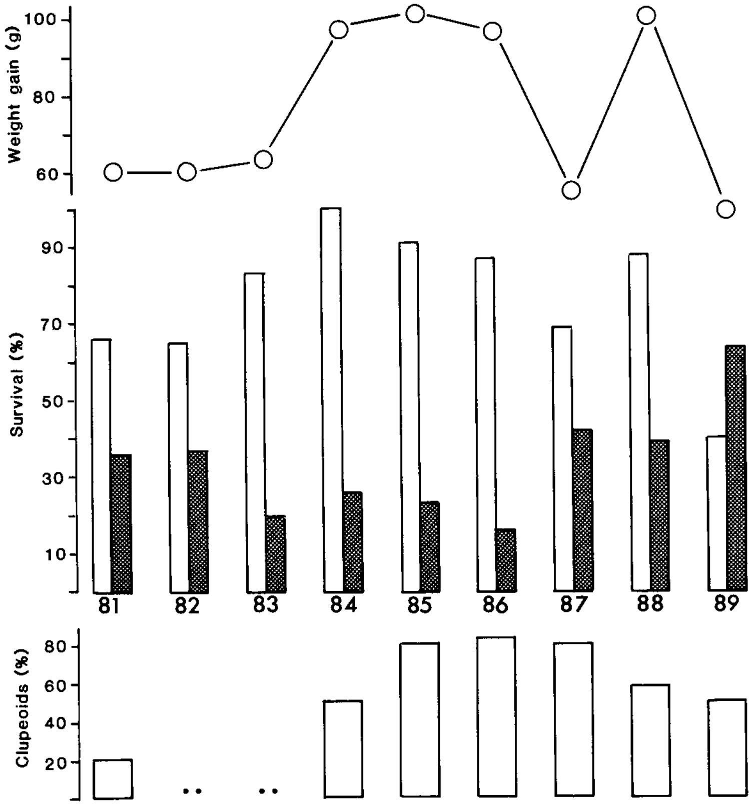

Fig. 9. Relationship between chick growth (graph; weight gain by the 7th day of life, data from Table 1), chick survival (from egg-eating+starvation, upper white columns; from other mortality factors, stippled columns; calculated from the original data in Table 1), and the percentage proportion of Clupeoids in chick regurgitations (lower columns) in 1981–89 (no data on food castings available in 1982–83). Only in 1981, were both the growth rate and the Clupeoid proportion significantly different from the corresponding figures in the best growth/feeding year 1985 (Mann-Whitney U-test, two-tailed P = 0.004; Fisher's exact test, P = 0.094). Note that in the years of good survival from egg-eating+starvation the survival from other mortality factors remains low.

ent ways in different years. The adult counts provided no clear evidence of non-breeding in the study colony (Hario 1989), but the mean clutch size tended to be smaller in years of elevated egg-eating frequency ($r_s = -0.673$, $P = 0.043$), this being further evidence of food-related factors (via courtship feeding).

As the estimated biomass of the spawning stock of Herring in the Gulf of Finland shows a continuous upward trend all through the 80s (Anon. 1989) the situation at Söderskär is not analogous to that in the Northeastern Atlantic, where the chick starvation (up to 70% in Arctic Terns *Sterna paradisaea*, Uttley et al. 1989) could readily be related to lows in the preferred prey fish stocks (Monaghan et al. 1989, see also Hislop & Harris 1985).

Starvation of chicks has been reported in several gull studies, the results emphasizing the parents' insufficient rate of provisioning for the whole brood (e.g. Harris 1964, Haycock & Threlfall 1975, Barrett & Runde 1980, Galbraith 1983, Thomas 1983, Murphy et al. 1984). The loss of younger siblings in favour of the older ones in times of food shortage is related to the asynchronous hatching of chicks, this being an important consideration in the brood reduction theory (e.g. Reid 1987). This is closely linked with the theory of optimal working capacity, i.e. a relationship between elevated breeding effort and decreased subsequent survival of parent birds (Royama 1966, Wooler & Coulson 1977, Drent & Daan 1980).

In these considerations, both the parents and the brood are modulating their response to the level of food situation. The behaviour of the inefficient parents in the present study differs sharply from this "prudent" response in that none of the chicks in a brood was fed. According to the latter theory the costs of reproduction had become so high that neglect of chick feeding was beneficial to the parents.

Two suggestions can be made: First, neglect of the brood is a rough remedy for those individuals whose survival is jeopardized whenever the food situation becomes "worse-than-average". Second, some harmful change has taken place in the birds' physiology, something which falls outside the scope of the theories of prudence. The damaging effects of organochlorine pollutants could well be involved, though the fitness and ultimate survival of the affected gulls is only partly understood (Fry et al. 1987).

It may well be that both these suggested explanations are valid for the Lesser Black-backed Gulls in the Gulf of Finland. The severe drops in the numbers of colony-attending adults in the 1980s also implies elevated adult mortality on the wintering grounds (Hario 1989). The proportion of inefficient pairs is rather high (9% in 1988 in the whole Söderskär area). Studies on the possible joint reason for these anomalies are urgently needed. The nominate race of the Lesser Black-backed Gull is decreasing rapidly over most of its breeding range (e.g. Kilpi et al. 1980), which itself is small and restricted to the Baltic and northern Scandinavia (Barth 1975).

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Selostus: **Suomenlahden selkälokkien huono pesimätulos: yhteys ravinnonsaantiin**

Vuosina 1980–89 Porvoon mlk:n Söderskärin selkälokit tuottivat keskimäärin 0.20 lentopoikasta/pari ja vähenivät noin kymmenen prosentin vuosivauhtia. Väheneminen johtui osaltaan kasvaneesta aikuiskuolevuudesta pesimäajan ulkopuolella.

Muna- ja poikastappiot olivat huomattavan suuria. Tutkimusyhdyskunnan munista tuhoutui vuosittain keskimäärin 36% ja poikasista 86%. Emot söivät munista keskimäärin 16% (vaihteluväli 0–52%), ja keskimäärin 13% poikasista jätettiin ruokkimatta (0–25%). Vastaavaa ei todettu Söderskärin harmaalokeilta, jotka hautoivat ja ruokkivat hyvin.

Molempien lokkilajien pääravintona oli silakka; selkälokin poikasten tuoreista oksennuksista 72% sisälsi silakkaa. Ravinto haettiin pääosin ulkomereltä, eikä poikasia saalistelevien harmaalokkien läsnäolo pesimäyhdyskunnassa estänyt selkälokkiemoja lähtemästä ravinnonhakuun. Palatessaan kuitenkin lähes 10% emoista jätti poikasensa ruokkimatta. Poikasten ravinnonkerjuukäyttäytymisessä ei ollut vikaa.

Omien munien syönti, nälkiintyneiden poikasten osuus ja ruokittujen poikasten kasvuvauhti korreloivat keskenään: mitä enemmän munia syötiin ja mitä useampi poikanen jätettiin ruokkimatta, sitä huonommin kasvoivat jäljelle jääneet poikaset. Nämä kolme tekijää eivät kuitenkaan korreloineet vuosittaisiin silakkakantojen koon arviointituloksiin; arviointien mukaan silakkakannat kasvoivat Suomenlahdella läpi 1980-luvun.

Söderskärin selkälokeilla ei näytä olevan syytä potea suoranaista ravintopulaa. Ravintotilanne saattaa kuitenkin laukaista käyttäytymishäiriöt fysiologisen stressin kautta (ympäristömyrkkykuormitus?), jolloin jokin ravintoekologinen seikka tahdistaa pesimämenestyksen vuosivaihteluita. Yhtä hyvin vuosivaihtelut voivat kuitenkin olla ravintotilanteesta riippumattomia, jolloin mahdolliset fysiologiset muutokset ilmenevät samoissa yksilöissä eri teholla eri vuosina.

Selkälokin huonon pesimämenestyksen syistä emojen käyttäytymishäiriöt ei kuitenkaan ole merkityksellisin, vaan suurimmat tappiot aiheutuvat poikasten sairauksista ja harmaalokin saalistuksesta.

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