

Dying in the midst of plenty — the third-chick fate in nominate Lesser Black-backed Gulls *Larus f. fuscus*

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In most studies on ground-nesting large gulls, there has been a common consensus that the death of the C-chick is the outcome of preferential feeding of larger chicks by the parents. The functional mechanism of this third-chick disadvantage would then be starvation or other starvation-induced mortality factors (notably predation). We have previously shown that the primary cause of death of necropsied C-chicks in three gull species in the Gulf of Finland was not starvation but rather innate diseases due to degenerations and inflammations of the liver and other internal organs. It remained to be seen, however, whether undernourishment due to poor competitive ability, i.e. the starvation effect, would lead to early outbreak of diseases. In the present study, we examined the chick–parent interactions in the nominate Lesser Black-backed Gull *Larus f. fuscus* by video recording the feeding instances at ten nests during the first four days of the C-chick's life. No evidence was found for behavioural discrimination against the C-chick. Those C-chicks that subsequently died of a disease were no less likely to be fed than the healthy C-chicks or the A- and B-chicks, but they were too weak to digest. This led to a wasting syndrome, most strikingly expressed by the rapid loss of body weight.

1. Introduction

Most gull species lay a modal clutch of three eggs. The last-laid egg, the C-egg, is typically smallest and hatches last (Paludan 1951, Parsons 1969, 1970, 1975, Lundberg & Väisänen 1979). The C-chick, if hatched, dies first or shows the lowest growth rate within its brood.

Studies on the functional mechanism of this “third-chick disadvantage” in gulls have been based mainly on egg or chick swapping experiments. They have focused on the external properties of the sibs (size asymmetry, hatching asyn-

chry) without being able to address the differences in physiological properties among the sibs. One common feature in the various studies has been that the A- and B-chicks, after all, fare better than the C-chick even when the C-chick has been made to hatch synchronously and equal-sized to its foster sibs (see e.g. Parsons 1970, 1975, Hahn 1981, Hébert & Barclay 1986, Royle & Hamer 1998). Survivorship of the C-chick can be made to equal, but not to exceed, that of the elder sibs in initial position of the brood hierarchy.

Ecological explanations for the third-chick disadvantage follow the lackian hypothesis of adap-

tive brood reduction (Lack 1947, 1954). They claim asynchronous hatching adaptive in the event of food scarcity. However, experimental studies have often failed to demonstrate lowered fledging result of artificially synchronized broods, which has been thought to result from focal feeding conditions being too benign for the adaptive brood reduction to emerge (for reviews, see, e.g. Forbes 1994, Stoleson & Beissinger 1995, Stenning 1996).

Despite the well-documented occurrence of the poor C-chick fate in gulls, few studies attempt to document the nature of this disadvantage. In gull studies, the third-chick disadvantage is said to result from parents systematically expelling the chick(s) in which they have invested the least or that will require the most future investment (Hahn 1981, Hébert & Barclay 1986). Nestling size-hierarchy, resulting from hatching asynchrony and egg-size asymmetry, is said to enable the parent birds to "target" the smallest chick in feeding and, in the event of food scarcity, eliminate it through starvation without having to recognize it individually (Hébert & Barclay 1986). This elimination is said to happen either by parents feeding at a distance from the nest, this hampering the youngest chick's chances to reach the food (Graves et al. 1984), or the parents, when regurgitating the food, move about and make the chicks chase them; the smallest and slowest chick would then be in competitive disadvantage to its elder sibs (Hébert & Barclay 1986, but see Pierotti & Bellrose 1986, Sydeman & Emslie 1992).

In our earlier studies on pathogens of three gull species in the Gulf of Finland, we found a high frequency of diseases affecting particularly the last-hatching chick, the C-chick. We then questioned the C-chick deaths as being merely starvation-induced (Hario & Rudbäck 1996), but were unable to exclude the possibility of parental-induced mortality, i.e. a systematic expelling of the youngest chick from then on after the very first feeding bouts.

In the following, we will take a pragmatic approach to chick elimination by looking what happens at Lesser Black-backed Gull *Larus f. fuscus* nests when the C-chick is starting to lose weight. As in many other gull studies, the ambient food levels are known (they were seemingly high, Hario 1997, or exceedingly high when judged from the

exploratory pelagic trawling of clupeoids in Finland, Anon. 1998), but we cannot manipulate food acquisition for the parents (e.g. Barrett & Runde 1980, Viksne & Janaus 1980, Braun & Hunt 1983, Burger & Gochfeld 1983, Galbraith 1983, Hamer et al. 1993, Hillström et al. 1994, Kilpi et al. 1996, but see Oro et al. 1995, 1996). Therefore, we do not aim to qualify or disprove the brood reduction hypothesis itself. However, we re-evaluate some of the methodological aspects of the past which have been used to link the third-chick fate to the premise of the hypothesis.

2. Material and methods

The study was made in June 1996 at the Söderskär Game Research Station, in the outer archipelago of the central Gulf of Finland (60°07' N, 25°25' E). In the local gulleries, we video recorded feeding instances at ten randomly selected Lesser Black-backed Gull nests during the first 4 days of chicks' lives. In three of these broods, the C-chick soon started to lose weight (broods assigned to "diseased" in Results), in the seven remaining broods all the three chicks grew well ("healthy" broods).

The chicks were individually dyed at hatching with a commercial non-toxic dye, so that a slight tinge of red or green on the throat and ventral region was discernable on the video. The chicks were ringed within 3 days of hatching and their weight gain was monitored daily (with a spring balance to the nearest 1.0 g). Their sequence in the clutch was known from direct observation (for the rest of the field work procedures, see Hario 1994, Hario & Rudbäck 1996).

The video recording was made from a portable hide at a distance of 3–8 m from the nest. Each nest was watched for 2 hours at a time. The recording sessions were rotated so that every nest was observed for a total of 3–5 hours, depending on how long the C-chick lived. Because the fate of the broods varied widely, it was not possible to equalize the length of recordings at each nest.

The feeding of the small chicks always took place at or close to the nest (within 1–2 m). The parents regurgitated the food bolus on the ground in front of the brood. From the video tapes we subsequently analysed:

- which one(s) of the chicks solicited feedings,
- how many feedings each chick attended, i.e. had free access to the food bolus (“meal-attending frequency” in Results),
- how often a chick failed to eat despite attending the meal (“eating frequency” in Results), and
- how did the parents respond to chick solicitings.

Because only one behavioural aspect was studied (the possible parental neglect), we do not consider variations in the timing of breeding, nor the egg-size asymmetry nor the hatching asynchrony (these traits are not the reasons for the claimed parental neglect, only a premise of the brood reduction hypothesis). We will, nevertheless, briefly address these issues in the Discussion and therefore give the relevant data in Appendix 1.

The cause of death of the three diseased C-chicks was examined at the National Veterinary and Food Research Institute in Helsinki (for methods, see Hario & Rudbäck 1996). The 27 remaining chicks of the study broods were taken by predatory Herring Gulls *Larus argentatus* or disappeared. Predation was confirmed by locating chick rings in the predator’s territory, and from direct observation.

In analyzing the behavioural data, non-parametric tests were used (Friedman test, chi-square test). Although a total of 10 nests were monitored, not all behavioural aspects could be recorded at all nests; therefore, the sample size varies. Results are given for those comparisons only in which all the three sibs in a brood were simultaneously present (i.e. still alive). As the magnitude of field work behind every sample (nest) varies, the Friedman statistic is used to test that there is no systematic variation in the rankings across scores. Each nest (brood) was used as a block (n) and sib order (A, B and C) was used as the experimental group (k).

3. Results

3.1. Chick solicitings

From the video tapes it became evident that it was not always possible to distinguish which chick

tried to solicit feeding. The begging behaviour of small chicks was obscure, incomplete or totally absent; in fact, parents frequently initiated feeding without gaining any apparent stimuli from the chicks. Of the 27 feedings recorded, 14 seemed to happen without chick solicitings. Of the remaining 13 feedings, begging was initiated by the A-chick in 5 cases, by the B-chick in 3 cases, and by the C-chick in 5 cases. Of the latter ones, 3 cases concerned diseased C-chicks.

At every feeding bout, parents regurgitated more food than could be consumed by the brood. From the enormous lump of half-digested food, the tiny chicks were able to consume only a small portion before ceasing to respond. The parent frequently re-swallowed the food and, after a while, offered it again. They could repeat this three to four times within a few minutes. In our results, we consider these multi-feedings as one. Hatch order did not affect the meal-attending frequency; chicks always had plenty of time to reach the food (Friedman test, $Fr = 0.143$, $P = 0.705$, $n = 10$). Thus, hatch order had no effect on the likelihood of parents feeding a chick. The food offered was always fish, notably Baltic Herring *Clupea harengus* (the species recorded at 24 instances).

3.2. Diseased vs. healthy broods

The diseased chicks had completely free access to the food, but instead of eating they often sat apathically by the food giving no apparent response, or, after having taken some food, began to convulse and vomited it out. Hatch order affected the eating frequency significantly ($Fr = 14.893$, $P = 0.021$) in that the diseased C-chicks had significantly lower eating frequency (13%) than the healthy C-chicks (85%, Yates corrected $\chi^2 = 7.78$, $P = 0.005$, Fig. 1). No significant differences emerged between their sibs (A-chicks: $\chi^2 = 1.055$, $P = 0.304$, B-chicks: $\chi^2 = 0.394$, $P = 0.530$), although one brood apparently contained diseased sibs (see below).

At necropsy, the alimentary track of the diseased C-chicks was empty, and they had inflammatory lesions in the yolk sac and intestine, and gastric ulcers in the gizzard. Clearly, they were severely ill, and starvation was not their primary cause of death. Instead, they were too weak to

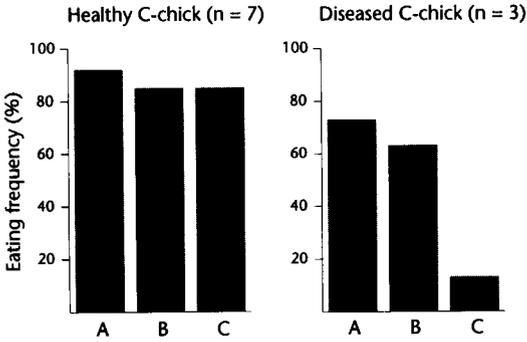


Fig. 1. Eating frequency (% of occurrence) according to hatch order (A-, B- and C-chicks) in healthy vs. diseased broods of Lesser Black-backed Gulls. "Diseased C-chick" denotes broods containing at least one diseased chick, usually the C-chick (for details, see the text).

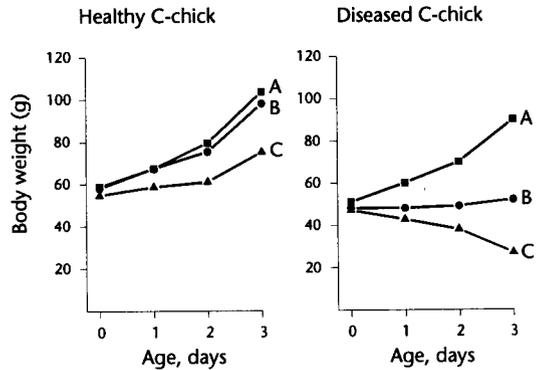


Fig. 2. Weight gain of Lesser Black-backed chicks according to age. Same samples as in Fig. 1.

digest.

During their first 4 days of life, the diseased C-chicks constantly lost weight whereas all the healthy chicks gained weight (Fig. 2). Of the broods containing a diseased C-chick, one also had an apparently diseased B-chick, its body weight gradually declining. This had a pronounced effect on the mean weight curve of the B-chicks of the "diseased broods" in Fig. 2. This chick fell the victim of Herring Gull predation at the age of 4 days and was therefore not necropsied. Herring Gull predation was the main mortality factor in the study colony. Verified predation (ring found in predator's territory or predation seen) took 11 study chicks, i.e. 37%. Another 16 chicks disappeared and were most probably taken, but their rings could not be located. All the rings found were in one single territory on a nearby islet, 200 m away. (The rate of verified predation, 37%, is now higher than the mean assessed predation rate of 21% in 1991–93 at Söderskär Lesser Black-back gulleries (Hario 1994), indicating that predation is becoming an increasingly severe problem for the declining Lesser Black-backed Gulls.)

4. Discussion

We found no evidence of behavioural discrimination against those C-chicks that lost weight and subsequently died of innate diseases. On the contrary, they seemed to be equally able and willing

to solicit feedings, and parents made no discrimination when responding to their begging. However, they failed to eat, not because of the lack of sufficient food or lack of access to the food, but because they were too sick to digest. Their prudent begging behaviour, however, seemed to mask their severe illness from the parents, who continued to release feedings for as long as a chick was able to solicit and/or get to the food, notwithstanding the fact that it just sat by the food bolus watching the healthy sibs eating. Only when a diseased chick ceased to respond by falling asleep and gradually losing consciousness prior to death did the parents lose their interest in feeding it. Parents never tried to wake up a "sleeping" chick. Then death was only a matter of a few hours or less. Death from a disease was an externally peaceful death.

The parents did not discriminate against the healthy C-chicks either. Our results agree with those of Davis and Quinn (1997). In their direct observations, Herring Gull C-chicks were not less likely than their older siblings to get to the food first, and, despite their smaller size (or because of it), were more aggressive and pecked siblings the most. No post hatching behavioural bias from parents or siblings against them was found, and Davis and Quinn (1997) conclude that interactions over food might "possibly not be the relevant parameter to study" (when dealing with parental investment and brood reduction in gulls).

Davis and Quinn (1997) also noticed the failure of eating by some of the Herring Gull chicks in the vicinity of the food bolus. Their impression

was that the chicks simply were not hungry. They did not address the mortality factors in their study, however.

Without the results of thorough necropsy and a record of parent-chick interactions, the C-chicks that died in our study could be claimed to have succumbed to starvation. Slow growth and low body weight have commonly been viewed as symptoms of starvation. Although seldom actually verified, the possibility of starvation seems obvious, and its potential for immediate impacts on Lesser Black-backed Gull populations has readily and uncritically been acknowledged (e.g. Strann & Vader 1992, Pons & Yésou 1997).

However, rapid weight loss is a symptom of a wide variety of physiological disorders and is strongly correlated with dehydration, not necessarily induced by food deficiencies. In our earlier study on chick mortality in three Finnish gull species (Hario & Rudbäck 1996), we demonstrated a high frequency of chick diseases due to degeneration and inflammation of various internal organs. C-chicks were most heavily affected in each of the three species: 73% of all victims in Herring Gulls, 75% in Lesser Black-backed Gulls, and 50% in Common Gulls *L. canus*. The reasons for the diseases affecting particularly the last-hatching chicks are unknown. The diseases may stem, e.g. from the biochemical processes embedded in vitamin mobilisation in the body, disorders of which cause increased susceptibility to infections. The causal agent involved, entering the chick from the female via the yolk sac, is unknown, but the infections themselves are very commonplace and the final cause of death is sepsis due to normal bacteria flora entering the blood system.

Chicks dying first are usually the smallest ones. The diseased chicks in this study tended to be lighter at hatching than the healthy ones (Appendix 1, Mann-Whitney $U = 1.60$, $P = 0.10$), but their egg-size asymmetry (the percentage difference of volume between the C-egg and the A-egg) did not correspond to the difference (Appendix 1). We had earlier found that egg-size asymmetry and timing of breeding did not predict the occurrence of chick diseases in three species of gulls (Hario & Rudbäck 1996), but that hatchling weight tended to be lower in chicks that subsequently died.

Despite suggestions in the literature to the con-

trary, parents appear to treat all chicks equally (see Davies & Quinn 1997). We argue that the claimed intentional “killing” through selective starvation in brood reduction has never been proved. The prevailing hypothesis assumes chick death to be associated with causes of starvation, but there is hardly any unequivocal evidence of that. Mortality is merely assumed to be “due to starvation”, or the victims are said to be “emaciated” or “appeared to have starved”. No proper post mortem examination for cause of death has been performed in any of the studies dealing with brood reduction in gulls.

As a whole, studies aimed to test the brood reduction hypothesis have yielded deviating results (for reviews, see Stoleson & Beissinger 1995, Stenning 1996). The problems arise from the interpretation of “good” and “bad” food years (e.g. Forbes 1994). Yet, before assigning causality to feeding conditions, other mortality factors than starvation must also be considered. Dying in the midst of plenty is not adaptive. This applies especially to gulls with ample access to high quality food over most of their range.

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Selostus: Kuolema keskellä yltäkylläisyyttä — selkälökin pahnanhajon kohtalo

Linnuilla pesyeen viimeisenä kuoriutuva poikanen on yleensä pienin, sen kasvu on hitainta ja kuolevuus suurinta. Jollei se kuole jo poikasvaiheessa, sen odotettavissa oleva elinikä jää myöhemminkin lyhyemmäksi kuin sisarussten. Poikasvaiheen kuolemisen yhtenä (kuuluisimpana) evolutiivisena selityksenä on pesyeen pienentämisen -hypoteesi, joka pelkistettynä tarkoittaa sisarusparven numeerista pienentämistä ravintotilanteen mukaan. Huonon ravintotilanteen vallitessa pienin poikanen, johon on panostettu vähiten, uhrataan isompien hyväksi, mikä tekee ilmiöstä adaptiivisen. Useita muitakin hypoteeseja on kehitelty selittämään ilmiön adaptiivisuutta tai epäadaptiivisuutta. Yh-

teistä näille on se, että emot aloittamalla haudonnan pesyeen ensimmäisestä munasta aiheuttavat kuoriutumisen epäsynchronian, jolloin pahnepohjimmainen on jonkin aikaa havaittavasti nuorempi kuin sisaruksensa ja helposti tunnistettavissa. Toiminnallisena mekanismina sen eliminoimisessa on emojen ja/tai sisarusten harjoittama syrjintä ravinnonjaossa tai suoranainen aggressio sitä kohtaan. Poikasen paino laskee, ja se näyttää kuolevan nälkään.

Lokkien kolmimunaisissa pesyeissä nimenomaan kuoriutumisenjärjestys osoittaa kuopuksen paikan pesyeessä. Söderskärillä selkälökin viimeisenä kuoriutuvan poikasen, C-poikasen, munan suhteellinen koko tahi kuoriutumispäivä eivät enustaneet poikasen kohtaloa, ainoastaan poikasen paino ja kuoriutumisenjärjestys (Liite 1). Pesälle "näлкиintyneinä" kuolevista selkälökin poikasista 75 % on ollut C-poikasista, mikä pintapuolisesti ajateltuna sopii hyvin pesyeen pienentämisen hypoteesin premissiin. Kaikissa tutkituissa Söderskärin poikasissa on kuitenkin ollut runsaasti sisäelinsairauksia, ja lopullinen kuolinsyy on ollut verenmyrkytys. Kaikkien ruoansulatuskanava on myös ollut tyhjä (Hario & Rudbäck 1996).

Kesällä 1996 videokuvassimme selkälökin poikasten ruokintaa Söderskärillä tarkoituksenamme eritellä, missä määrin C-poikasen tautitilojen synty saattaisi juontua ruokkimattomuudesta tai aliravitsemuksen tuottamasta stressistä eli pesyeen pienentämisen hypoteesin mukaisesta syrjinnästä. Kuvassimme poikasten ruokintaa kymmenellä pesällä C-poikasen neljän ensimmäisen elinpäivän ajan. Videonauhoilta analysoimme mm., kuinka moneen ruokintaan pesyeen kukin poikanen osallistui ja millä tuloksella. Kymmenestä kuvatusta pesyeestä kolme oli sellaisia, joissa C-poikanen ei syönyt (Kuva 1) siitä huolimatta, että se tasaveroisesti asettui aterialle ja samalla tavoin kuin sisaruksensa käärtämällä laukaisi emon ruokintakäyttäytymisen. Muiden syödessä se seisoi aloillaan ruoan äärellä. Jos se ottikin ruokaa, se ei pystynyt nielemään tai oksensi sen pian ulos. Paino kääntyi heti laskuun (Kuva 2), ja poikanen kuoli muutamassa päivässä. Sen ruoansulatuskanava oli tyhjä, ja kuolinsyynä oli yllä kuvatut tautitilat. Aktiivista syrjintää ruokintatilanteissa emme pystyneet toteamaan yhdelläkään pesällä. Päätelemme, ettei C-poikasten korkea tautikuolleisuus Söderskärillä johdu syrjinnästä eikä liity poikueen pienentämisen

-ilmiöön. Lökkikirjallisuudesta emme löytäneet yhtäkään tapausta, jossa nälkäkuoleminen olisi sitovasti osoitettu, koska yhdessäkään tapauksessa poikasille ei ollut tehty ruumiinavausta. Toistaiset harvat käyttäytymisekologiset työt ovat päinvastoin osoittaneet, ettei aktiivista syrjintää tapahdu. Pesyeen pienentämisen hypoteesin adaptiivisuuden lähtökohta (ravintotilanne) voidaan lokkitutkimuksissa kyseenalaistaa.

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Appendix 1. Differences in timing of breeding (hatching initiation), egg-size asymmetry (%) and C-chick hatchling weight (g) between broods of healthy chicks and those containing at least one diseased chick at Söderskär in 1996. Mean \pm SD (N).

Timing of breeding, date		Egg-size asymmetry		C-chick hatchling weight	
Diseased	Healthy	Diseased	Healthy	Diseased	Healthy
18.6. \pm 9 (3)	18.6. \pm 7 (7)	4.17 \pm 3.02 (3)	5.49 \pm 2.73 (7)	47.0 \pm 2.6 (3)	54.0 \pm 3.4 (6)