

# Effects of supplementary feeding on the C-egg constituents in the nominate Lesser Black-backed Gull *Larus f. fuscus*

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Providing extra food next to the nest of laying Lesser Black-backed Gulls of the nominate race *Larus f. fuscus* in the Gulf of Finland did not result in differential lipid, nitrogen or protein proportions in the C-egg compared with a control group of similar median laying date. The amount of extra food received varied among females, but the relative size of the C-egg was not positively correlated (the volume of the C-egg in relation to that of the A-egg). The courtship feeding rate correlated positively with the female territory attendance, i.e. females that spent much time at the territory received many courtship feedings. This was because their success in soliciting feedings was high compared with those that were often absent (as measured by the number of female beggings/released feeds by the male). Hence, being absent might be a consequence of a low courtship feeding rate rather than the reason for it. Whatever the case, long absence and a low courtship feeding rate did not lead to a decrease in egg-size asymmetry, rather, the contrary. It is concluded that foraging independently may be a more important option for a laying female than a heavy reliance on the male's courtship feeding activity, especially under benign foraging conditions. The supplementary feeding regime had little discernible effect on the feeding behaviour of gulls, which might be a further indication of locally plentiful food stocks (i.e. Baltic Herring *Clupea harengus*).



## 1. Introduction

Experimentally increasing the food supply has led to higher egg production in several wild bird species. Providing extra food to the laying female advances the laying date and may lead to an increase in clutch size relative to the number predicted by the timing of the laying (Ewald & Rohwer 1982, Arcese & Smith 1988, Beukeboom et al. 1988, Meijer et al. 1990). Studies on Lesser Black-backed Gulls *Larus fuscus* of the atlantic race *graellsii* have yielded deviating results, viz.

an increase in clutch size independent of the laying date (Hiom et al. 1991, Bolton et al. 1992, 1993). One hypothesis is that the clutch size of Lesser Black-backed Gulls is determined primarily by the amount of the pre-laying body reserves of the female (Bolton et al. 1992, see also Houston et al. 1983), and that egg size, on the other hand, may be largely influenced by dietary intake during the period of egg formation (Bolton et al. 1993).

A useful indicator of the female's nutrient reserves might be the relative size of the egg laid

last (the C-egg) compared with the first one (A-egg). This egg-size asymmetry has been shown to correlate with fledging success. Kilpi et al. (1996) did not find any effect of egg size *per se* on the early mortality of chicks in the Herring Gull *Larus argentatus* but found instead a significant correlation between egg-size asymmetry and fledging success; i.e. the smaller the C-egg relative to the A-egg, the lower the probability of fledging (see also Kilpi 1995). They also suggest a gradual shift from no asymmetry via increasing asymmetry to finally not laying a third egg. Egg size would thus be the first factor affected under poor feeding conditions (see also Bolton 1991).

The relative size of the C-egg is influenced by the amount of albumen in the egg (Parsons 1976), more albumen means a larger egg and absolutely more energy in terms of increased albumen protein (Meathrel & Ryder 1987, Meathrel et al. 1987). A large egg produces a larger hatchling with greater prospects of survival compared with a smaller egg (e.g. Lundberg & Väisänen 1979, Williams 1994). Albumen proteins are thought to be derived from exogenous nutrients during laying, though the conversion efficiency of endogenous vs. exogenous nutrients into egg production is poorly known in most species (Houston et al. 1995b).

Courtship feeding by the male makes one source of exogenous nutrients available to the female gulls prior to laying. In Herring Gulls, the lipid reserves in the male decrease concurrently with the increasing reserves in the female prior to laying (Hario et al. 1991). This suggests that males allocate resources to territory defence, mate guarding and courtship feeding in favour of its mate's condition (for deviating results in terns, see Wendeln & Becker 1996). Males lost fat, not proteins. Females gained lipids, but subsequently invested them into eggs.

Salzer and Larkin (1990) showed that male Glaucous-winged Gulls *L. glaucescens* cease courtship feeding as soon as the first egg is laid. The larger the size difference between the C-egg and the A-egg, the lower the rate of male courtship feeding during the 2–3 days prior to laying of the C-egg (Salzer & Larkin 1990). Does this mean that the female has less food available to her during egg formation? The answer depends on which component in the C-egg was reduced:

yolk or albumen, and what nutrients. It also depends on whether or not the female is able (or willing) to provide herself with nutrients independently of the male's courtship feeding.

In this study I examine:

- whether within-clutch egg-size asymmetry in the nominate Lesser Black-backed Gull *L. f. fuscus* is influenced by differential courtship feeding rates between pairs,
- which constituents of the egg actually are reduced as the size of the C-egg decreases, and
- is the lower viability of the C-egg/chick related to food constraints during laying — a factor the female cannot affect.

My ultimate goal is to see whether supplementary feeding during the courtship period can be used as a management tool to improve the breeding success of nominate Lesser Black-backed Gulls. This gull has an exceedingly poor reproduction rate, and the populations have decreased over most of the subspecies' range (Hario 1990). In the Gulf of Finland, the poor reproduction rate results from a high rate of early chick deaths from diseases (Hario 1994, Hario & Rudbäck 1996). The diseases tend to be very simple: degenerations of and inflammations in various internal organs and accompanying sepsis. As in most gull studies, C-chicks were most heavily affected (75% of victims). Hario and Rudbäck (1996) concluded that there must be some innate factor entering the chick from the female via the yolk sac and affecting particularly the last chick hatched. This innate factor might be manifested in a deficiency of certain nutrient(s), perhaps measurable as differences in some of the egg constituents of supplementary fed and non-supplementary fed birds.

## 2. Methods

The study was conducted at the Söderskär bird sanctuary, in the central part of the Gulf of Finland (60°07'N, 25°25'E) in 1993. The gulls nested on a grassy islet with patchy juniper cover on a central boulder ridge. The nests were sited close to the shore, in short grassy vegetation between boulders and larger rocks. The closest neighbours were Arctic Terns *Sterna paradisaea*, Black Guillemots *Cephus grylle* and a few Herring Gulls.

I began observations in early May during territory occupation and continued through the chick-rearing period and fledging in early August. Laying was surveyed by daily visits and by observations from a blind (see Section 2.1.). Nest constructions were marked as soon as they were located (with a numbered wooden stick), and eggs were marked (on the blunt end) in waterproof ink with their ordinal number in the clutch (A-, B- and C-egg).

## 2.1. Recording time budgeting and courtship feeding rate

From a wooden hide, placed on a rock ledge and overlooking the entire subcolony of 18–20 pairs, I checked the arrivals and departures of every study individual throughout my observation sessions. I also recorded all instances of females begging for food and males providing it, and whether or not the target female received the food supplement.

The watches lasted on average 2.5 hours (range 1–5 h) for a total of 146 h or 2 190 nest-h of observation. They varied between the morning one day, midday the next, and afternoon–noon the third. This rotation allowed for most of the daylight hours (between 06 and 22 h) to be covered fairly equally.

Courtship feeding and territory attendance was observed during 25 days around the laying. I divided the data into five periods: from 5 days prior to the laying start until the day before laying (Pre-laying II), 5 days preceding this (Pre-laying I), the laying period (2 days for each A-, B- and C-egg) and two subsequent 5-day periods after laying (Post-laying I and II). I was not able to extend the pre-laying study phase longer because nest building did not usually begin until 7 to 10 days before the first egg was produced.

Sex was determined from copulatory/courtship feeding behaviour, or by observing the relative size between mates. All birds were in full adult plumage, but the actual age was unknown. Most individuals were recognised on the basis of variations in bill markings and plumage; three experimental pairs were, however, colour-ringed from previous studies, and some had normal steel-rings.

For each pair, I calculated the percent time spent in the territory, separately for male, for female, for both parents together and for either parent at-

tending the territory alone. The two latter figures together give the combined percent of nest occupancy.

Courtship feeding rates were calculated as the number of feedings per hour during the time when both members of the pair were present. I chose this relationship instead of using the number of feedings per total observation time per pair (regardless of birds' presence) because I wanted to compare the feeding efficiency between pairs, not the differences in total provisions which are prone to ample stochasticity owing to the unknown number of courtship activities occurring outside the territory, out of my sight (Niebuhr 1981, Tasker & Mills 1981). I also wanted to make the results comparable with those of other studies. Nevertheless, I comment on the above-mentioned relationship when appropriate.

For one control pair, the courtship feeding rate could not be determined because the territory was partly out of sight (concealed by vegetation and large stones).

## 2.2. Provision of additional food

I provided 4 pairs with supplementary food consisting of cooked Herring Gull eggs made into an omelette (120 g/day each pair) and 3 other pairs with 120 g/day of commercial dog food. The caloric value of the dog food was 600 kJ/100 g, and the amount of crude protein was 14.5% and that of crude fat 9%. I did not determine the caloric value of the eggs, but assumed it matched the figure given by Drent (1970) of Herring Gulls, about 700 kJ/100 g. Seven other pairs were used as controls; they were not fed but were subject to the same amount of disturbance and observation as the experimental pairs. Timing of breeding did not differ between the two groups (median laying start in experimental nests on 15 May, in control nests on 16 May; Mann-Whitney,  $z = -0.315$ ,  $P = 0.752$ ).

The food was placed beside the nest at the beginning of each observation session in the hide. The feeding regime started 2–10 days prior to the laying start, or, at one nest, on the day the A-egg was laid. There was no way to predict the initiation of laying and therefore it was difficult to equalize the length of the supplementary feeding at each nest. In all cases, the feeding was stopped the day before the laying of the C-egg.

The laying span was 4–5 days; thus, each nest received additional food 4 to 15 times (Table 1). This did not, however, parallel with the amount of extra food actually received. From the hide I checked whether or not the target female got the food. Of the 56 supplementary portions of food provided, males initially took 21, and 14 of these were subsequently given to the female as courtship food (usually within one hour). Females initially took 14 portions, and in 7 instances both sexes ate the supplementary food together. In such cases, the female's share was approximated by eye. The remaining 14 portions (25.0%) were taken by neighbouring or prospecting gulls (not necessarily conspecifics). Of these, 3 portions were taken by control males, but as I never saw them give the stolen food to any females, I have ignored their possible effect. Converted into grams, females received 200–800 grams of extra food (Table 1).

### 2.3. Egg composition

At each experimental and control nest, the C-egg was removed as soon as it was laid, then hard-boiled, wrapped in plastic, and stored frozen for subsequent laboratory analysis. Egg measurements were taken and the volume and egg-size asymmetry calculated as described by Hario and Rudbäck (1996) (asymmetry = the percentage deviation of the C-egg volume from the volume of the A-egg).

Eggs were analysed for lipid, nitrogen and protein content. For analysis, egg yolk and albumen were separated, and lipids were removed by Soxhlet extraction using chloroform as a solvent. Nitrogen and protein contents were measured using the Kjeldahl Nitrogen method following the normal procedures (the commercial Kjeltex system I; % crude protein =  $N \times 6.25$ ). The results are given as percentages of dry weight.

Table 1. Number of days with supplementary feeding, the amount of extra food finally received by each female prior to and during laying (one portion provided/day, females nos. 1–4 had egg supplements, females nos. 5–7 had fat supplements), timing of laying, courtship feeding rate, and egg-size asymmetry of the supplementary fed and control birds (nos. 8–14).

Female no.	Days of suppl. feeding	Laying start	Laying span (days)	Food amount (g)			Courtship feeding rate	Egg-size asymmetry
				Prior to laying	During laying	Total food		
1.	9	10 May	4	300	200	500	0.36	-4.42
2.	5	12	4	150	200	350	0.43	-2.43
3.	11	20	4	300	350	650	0.10	-7.96
4.	6	20	4	-	300	300	0.12	+1.92
5.	4	13	4	-	300	300	0.78	-7.93
6.	6	15	4	-	200	200	0.29	-1.30
7.	15	26	5	500	300	800	0.97	-10.44
Mean		16.57						-4.56
S.D.		5.65						4.37
8.		10 May	4				0.13	-0.17
9.		24	4				0.29	-0.44
10.		14	4				0.58	-4.41
11.		16	4				0.63	-11.04
12.		16	5				0.42	-4.02
13.		18	4				0.48	-5.56
14.		19	4				..	-4.02
Mean		16.71						-4.24
S.D.		4.35						3.63

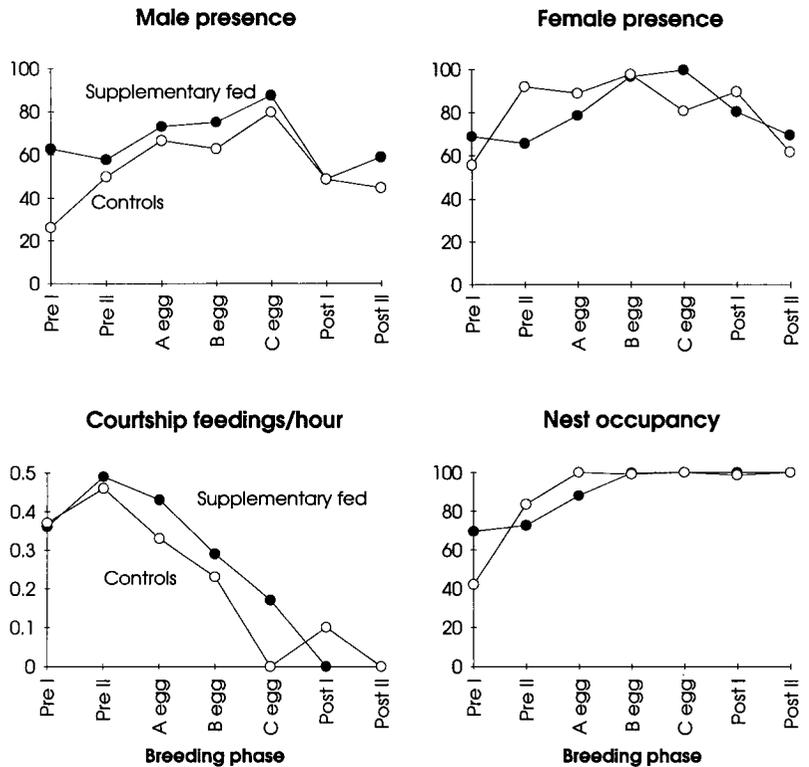


Fig. 1. Mean percent of time observed when males and females were present in the territory, their overall nest occupancy, and courtship feeding rate of supplementary fed (dots) and control (circles) Lesser Black-backed pairs during different breeding phases.

### 3. Results

#### 3.1. Territory attendance

There was no significant difference in territory attendance between the two groups of males and females during the entire study period (two-way ANOVAs accounting for the effect of breeding phase, males:  $F = 0.735$ , females:  $F = 0.894$ ,  $P > 0.1$ ), although the experimental males tended to spend more time in the territory than control males during the early part of the pre-laying period (Pre-I in Fig. 1). Upon the laying of the B-egg, the nest occupancy was 100% for both groups. There was a slight increase in the presence of the female in the control group from Pre-I to Pre-II, although this did not deviate significantly from the experimental group.

#### 3.2. Timing of courtship feeding

In both groups, the courtship feeding rate peaked at 1–3 days prior to the laying start and decreased

rapidly after that (Fig. 1); there were no significant differences between the groups during any of the breeding phases. The ratio of female beggings/released feeds was also about equal (3.04 vs. 3.06). Overall, 82 beggings led to 27 feedings during the 91.6 nest-hours when both members of the experimental pairs were present. The corresponding figures for the control pairs were 49 beggings and 16 feeds during 71.5 hours.

Of the 13 courtship meals where the food could be seen (supplementary food excluded) all had fish and in 12 of these it was Baltic Herring (*Clupea harengus*).

#### 3.3. Egg composition

There were no significant differences between the different treatments (egg supplements, fat supplements, controls) for any of the egg constituent proportions (Kruskal-Wallis ANOVA with Tukey Test) except for albumen lipids ( $H = 8.309$ ,  $P = 0.016$ ), which in the control group were higher than in the egg supplement ( $P = 0.016$ ) and in the

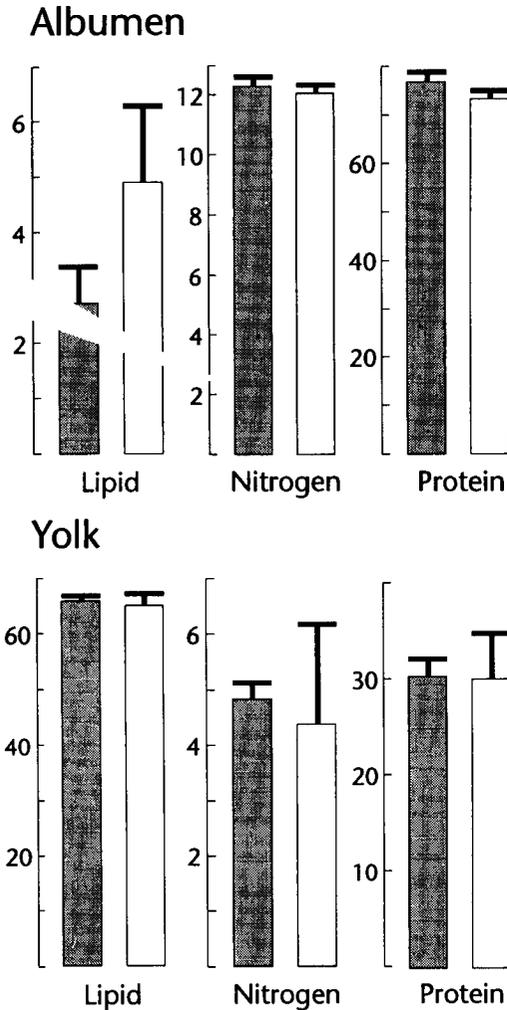


Fig. 2. Organic composition of the C-egg of the supplementary fed (dark columns) and control birds (white columns). % of dry weight, mean + S.D. N = 7 in both groups.

fat supplement group ( $P = 0.056$ ). The two latter groups did not differ from each other ( $P = 0.919$ ), and their results have been combined in Fig. 2.

Albumen lipids are present in very small amounts in avian eggs (representing less than 1% of fresh egg mass in poultry) and therefore generally omitted in studies (Meathrel & Ryder 1987, Meathrel et al. 1987). They probably have no functional significance here either, but this is difficult to evaluate.

Dry yolk consisted of 65–66% lipid and 30% protein in all groups, which represent a compar-

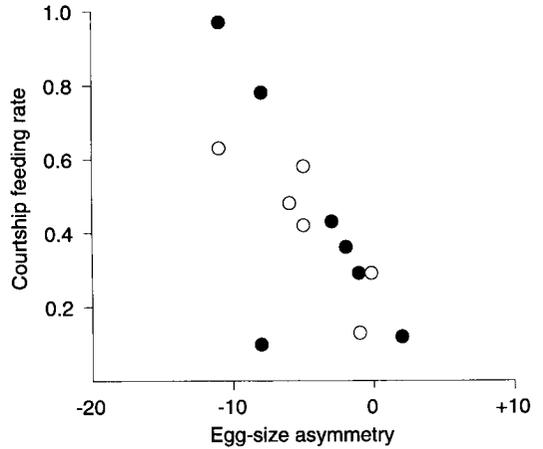


Fig. 3. Courtship feeding rate (feedings/hour when both partners present) during Pre-II phase inclusive laying period (totalling 10–11 days), in relation to the egg-size asymmetry of supplementary fed (dots) and control (circles) Lesser Black-backed pairs.

tively high energy content of an egg (cf. Meathrel et al. 1987).

### 3.4. Egg-size asymmetry and courtship feeding rate

The courtship feeding rate (feedings/hour when both partners were present) correlated negatively with egg-size asymmetry ( $r_s = -0.663$ ,  $N = 13$ ,  $P < 0.05$ ; Fig 3). This applied to both groups but was more pronounced in controls (Fig 3; controls:  $r_s = -0.943$ , experimental:  $r_s = -0.464$ ). The correlation remains negative ( $r_s = -0.40$ ) even when calculated from feedings/observation hours per pair, although it is merely suggestive. However, the courtship feeding rate correlated positively with the female territory attendance: females that spent much time on the territory received many courtship feedings ( $r_s = 0.516$ ,  $P < 0.05$ ). Conversely, females that were frequently absent received less courtship feedings. This holds even when the courtship feeding rate is calculated from hours that females spent in the territory, regardless of the males' presence (controls:  $r_s = 0.551$ ; experimental:  $r_s = 0.673$ ; Fig. 4). This was probably related to differential efficiency in soliciting feedings among females: female territory attendance correlated significantly with begging suc-

cess (no. of released feeds/begging instance) in both groups (controls:  $r_s = 0.56$ ; experimentals:  $r_s = 0.60$ ,  $P < 0.05$ ).

On the other hand, the courtship feeding rate did not correlate with the amount of supplements among females ( $r_s = 0.216$ ), so the supplementary feeding regime itself had little discernible effect on the feeding behaviour of the gulls. This is further illustrated by the fact that the amount of extra food a female received correlated negatively with her egg-size asymmetry ( $r_s = -0.757$ ,  $N = 7$ , 1-tailed  $P < 0.05$ ), i.e. the more extra food the female received, the smaller (proportionately) C-egg she laid.

#### 4. Discussion

##### 4.1. Supplementary feeding in relation to courtship feeding

The supplementary feeding regime in this study seemed to have little or no effect on the courtship feeding behaviour and nest occupancy of Lesser Black-backed Gulls. Though a spectacular event in a gull colony, courtship feeding is comparatively infrequent and highly irregular. Bolton et al. (1992) were unable to demonstrate any increase in the rate of courtship feeding in Lesser Black-backed Gulls' territories provided with additional food. The same was true in my study, notwithstanding the higher overall levels of courtship feedings. My levels were close to those of Burger (1986) in Herring Gulls (on average 0.3 feedings/hour per pair in the ten days prior to laying) and Mills (1994) in Red-billed Gulls *L. novaehollandiae scopulinus* (range 0.06–0.38). Those of Bolton et al. (1992) averaged only 0.03–0.05.

In my study, there were pairs that very seldom exhibited courtship feeding, even when the returning male had been away for several hours (which normally leads to noisy greeting ceremonies and female begging). My impression was that females, from the appearance of the male's gullet, could see whether or not he had food.

Instead of eating the supplementary food by themselves, many females waited for the male to eat and then solicited feedings. This apparent "failure" in exploiting the extra food independently of the male indicates that courtship feeding has its

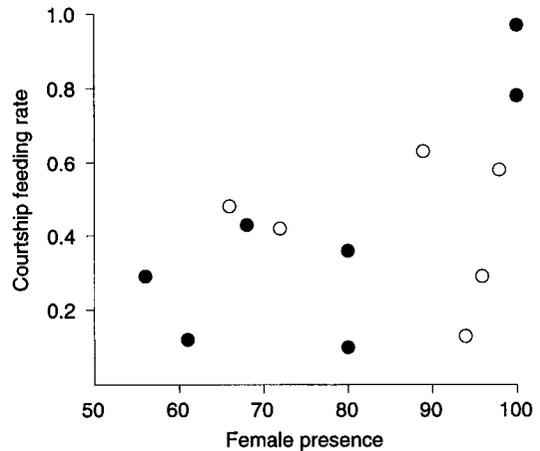


Fig. 4. Courtship feeding rate (calculated as in Fig. 3) in relation to the time female spent in the breeding territory (% of time observed). Symbols as in Fig. 3.

origin in pair-bond maintenance (as a pre-coital behaviour, Tinbergen 1953) rather than in providing needed food.

Nonetheless, many studies point to courtship feeding as being necessary for the production of eggs (e.g. Tasker & Mills 1981, Salzer & Larkin 1990). Whilst this has been shown in terns (Nisbet 1973, Wendeln & Becker 1996), there is less evidence in gulls. Tasker and Mills (1981) suggested that females who were less frequently fed during courtship spent more time foraging than females who received more food from their mates. They considered the former as being inadequately fed by their partner. My data suggest the same, but goes further in that "neglected" females with low begging/feeding rate and long absenteeism nevertheless laid proportionately larger C-eggs. Thus, females foraging for themselves may do better than those relying on the male's provision. Females who spend time in waiting for their mate may be losing time from effective food intake. In general, the frequency of courtship feeding has been low in many studies, indicating that its value as a food source is at least variable.

##### 4.2. Effects of supplementary feeding on egg production

The effects of supplementary feeding in larids have varied greatly among studies. Female Lesser

Black-backed Gulls of the race *graellsii* laid larger clutches and larger C-eggs when provided with extra food (Hiom et al. 1991). However, the increase in clutch size became discernible only in poor food years and only when the supplementary food was protein-rich rather than rich in energy, i.e. lipids (Bolton et al. 1992, 1993). The food conditions in a year were initially evaluated from the clutch size distribution, a low mean clutch size suggesting poor food availability (Hiom et al. 1991). However, Hiom et al. (1991) also showed that the egg-size asymmetry correlated with the clutch size variation among "good" and "bad" feeding situations. In a bad situation, the egg-size asymmetry was 13.2% but in a good one only 7%. In a bad situation, it was possible to diminish the asymmetry through supplementary feeding down to 8.6% (Hiom et al. 1991). In the Western Gull *L. occidentalis*, a range of 7.5–10.6% in asymmetry did not have any effect on the survival of the C-chick despite the correlation between the feeding environment and egg-size asymmetry (Sydeman & Emslie 1992).

In my study area, the egg-size asymmetry of the nominate Lesser Black-backed Gull ranks very low; the range of the annual means was 2.1–8.4 during 1990–1996 in the study colony. There was no between-year difference in the egg-size asymmetry (one-way ANOVA,  $F = 1.543$ ,  $df = 6, 82$ ,  $P = 0.175$ ), indicating that the feeding conditions at Söderskär are not sufficiently "bad" to result in the differences in gull egg production described elsewhere (sensu Bolton et al. 1992). In the study year 1993, the egg-size asymmetry in the entire colony averaged 5.8 (median 6.0) which did not differ significantly from the other years ( $F = 0.011$ ,  $df = 1, 87$ ,  $P = 0.918$ ).

Providing fat supplements during the 4–5 days of laying (commencing after the A-egg laying) reduced the egg-size asymmetry practically to nil in Glaucous-winged Gull, but there was no effect when supplements were provided for a median of 24 days prior to laying and ceased at laying of the A-egg (Reid 1987). No similar difference in effects was found by Hiom et al. (1991). Reid (1987) concluded that food limitation following the initiation of laying, not the energetic costs of egg formation prior to laying, was of prime importance as a clutch and egg-size determinant. Providing additional food enhanced the food intake

of the laying female during the critical period when the courtship feeding rate suddenly dropped as a result of a change in the behaviour of the male (presumably) to guarding its mate. However, in Reid's data, the simultaneous nest-attendance by both partners decreases sharply after clutch initiation, indicating that the other partner was, nevertheless, free to forage. Sexes were not separated in Reid's data, so the question remains open whether females really became food deprived.

In the data of Salzer and Larkin (1990), the courtship feeding rate did not cease altogether until some days after clutch completion. (The same is seen in my data.) In fact, they claim the highest effect of courtship feeding on the size of the C-egg 2–3 days prior to its laying, i.e. while laying the B-egg. This is, however, a by-product of their egg-removal experiments. The experimental pairs, losing the A-egg, continued the courtship feeding beyond the normal and contributed substantially to the rank correlation between courtship feeding rate and egg-size asymmetry. For control nests solely, there was no significant correlation, albeit it was negative (recalculated from table 2 in Salzer & Larkin 1990).

I have used the A:C-egg relation as the indicator of egg-size asymmetry. However, in one of the few studies where the annual food situation for the gulls could be assessed (through differential trawler discard availability), Oro et al. (1996) found the A-egg contributing most to the intra-clutch variation between years in the Audouin's gull *L. audouinii* (see also Ruiz et al. 1996, Brown & Morris 1996). Thus, the C-egg as a percentage of the A-egg could, in fact, increase when resources for egg formation were limited. However, in my study colony, the between-year variation of the A-egg size ( $F = 0.995$ ,  $df = 6, 82$ ,  $P = 0.434$ ) was even smaller than that of the egg-size asymmetry.

### 4.3. Supplementary feeding as a tool in enhancing the egg quality

Despite providing supplementary food consisting of animal protein (Herring Gull eggs), I was not able to confirm the results of Bolton et al. (1992) of Lesser Black-backed females being limited in the nutrients required for any of the egg constituents measured with the conventional methods. The

energy content of the C-egg was high in both study groups. Bolton et al. (1992) claim a protein limitation, but this was only detected in yolk, not in albumen (cf. Meathrel & Ryder 1987, Meathrel et al. 1987). Without doubt, these methods are too robust to detect to what extent gulls are actually depending on stored body reserves for egg formation and what is the role played by daily food intake during laying (for conversion efficiency of various nutrients into egg production, see Houston et al. 1995a, b). In addition, partitioning the specific nutrients, like essential amino acids, would require more sophisticated methods (Murphy 1994). Sacrificing individuals for investigations of nutritional requirements was not possible at Söderskär.

However, supplementary feeding trials have been effective only in years of poor feeding conditions. In the study year, no indications of poor feeding conditions were detected from the egg size variation, which could mean that my chances to detect significant differences were small or non-existent. The peak energy demand of egg laying in the Herring Gull is about 270 kJ/day during the 3–4 days prior to laying the first egg (Norstrom et al. 1986), so an extra food portion of 600–700 kJ/day (my supplementary food) should be of some benefit if females were food deprived.

#### 4.4. Concluding remarks

Females in this study did not seem to be dependent on feeding in the nesting territory, whether through supplementary feeding or courtship feeding. So far, convincing evidence of the courtship feeding rate being the main determinant of C-egg quality is lacking in nominate Lesser Black-backed Gulls.

In the study of Bolton et al. (1992), chicks hatching from the eggs of females provided with supplementary food such as eggs (protein-rich) did not, however, gain an advantage through enhanced survival. Their skeletal size and weight at hatching were larger than those of the controls, but any potential advantages from this was short-lived. Moreover, this applied only to the B-chicks (Bolton et al. 1992). This is puzzling because the frequently cited supplementary feeding trial of Reid (1987) affected only the C-egg size.

Summing up: there seems to be no way to alleviate the high chick mortality of nominate Lesser Black-backed Gulls by simply adding protein-rich food to the diet of laying females. The laying females are probably not food deprived in the ordinary macronutrients, and no studies in the literature so far give convincing evidence that gulls feeding on protein-rich fish (such as Baltic Herring) would not meet the protein requirements for egg formation of the modal clutch of three.

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#### Selostus: Keinollisen lisäruokinnan vaikutus selkälökin munien laatuun

Ruokkimalla selkälökkejä pesälle asetetuilla ylimääräisillä ravintoannoksilla ennen munintaa keväällä 1993 Söderskärillä yritettiin vaikuttaa pesyeen kolmannen munan, C-munan, rasva- ja proteiini-koostumukseen. Päivittäin tarjottiin 120 g koiranmakkaraa tai 120 g harmaalökin munasta valmistettua omelettia. Naaraiden saamalla ravintomäärillä ei kuitenkaan ollut toivottua vaikutusta C-munan keltuaisen ja valkuaisen suhteelliseen koostumukseen eikä munan suhteelliseen kokoon (tilavuuteen suhteessa A-munan tilavuuteen; Taulukko 1, Kuva 2). Naaraiden kosioruokintatiheys korreloi negatiivisesti munakoon kanssa (Kuva 3) ja positiivisesti naaraiden pesällä viettämään aikaan (Kuva 4). Tämä ilmentää naaraiden ravinnonsaannin vähäistä riippuvuutta kosioruokinnasta ja pesällä saatavasta ravinnosta. Naaraat, jotka viettävät paljon aikaa pesällä, ilmeisesti menettävät tehokasta ravinnonottoaika muualla odottaessaan koiraan paluuta. Lisäruokintakokeella ei juuri ollut havaittavaa vaikutusta lökkien ravinnonottoon, mikä saattaa olla seurausta vakaista ja hyvistä ravinto-oloista ympäristössä. Koe tukee osaltaan aikaisempaa johtopäätöstä siitä, että Söderskärin selkälökin poikasten korkea tautikuolleisuus ei johdu ravinnon määrästä.

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