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Is asynchronous hatching adaptive in herring gulls (*Larus argentatus*)?

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Abstract Hatching asynchrony commonly induces a size hierarchy among siblings and the resultant competition for food between siblings can often lead to starvation of the smallest chicks within a brood. We created herring gull (*Larus argentatus*) broods with varying degrees of hatching synchrony by manipulating the timing of incubation while maintaining the originally laid eggs. The degree of hatching asynchrony affected sibling size hierarchy at the time of hatching of the last-hatched “c-chick.” In unmanipulated broods, there was no disadvantage of being a c-chick. However, when asynchrony was experimentally increased, we found reduced survival of the c-chick only in the exaggerated asynchronous experimental group. The effects were observable only during the first 10 days of chick life. We recorded no cases of the chicks dying of starvation. Furthermore, behavioral observations indicated that there was no sibling competition, and no selective feeding of larger sibs in the study colony. We propose that the observed lower survival rates of c-chicks in exaggerated asynchronous broods resulted from their lesser motor abilities, affecting their chances of escaping predators. Fledging success for the whole colony was generally high and almost half of all pairs fledged all three chicks, which is indicative of a good feeding environment. We argue that normal hatching asynchrony is a favorable solution in a good feeding environment, but that increased asynchrony reduces breeding success. We do not view asynchrony in the herring gull as an adaptation for brood reduction and

propose instead that it may come about because there has been selection for incubation to start before clutch completion.

Key words Hatching synchrony · Brood reduction · Feeding behavior · *Larus argentatus* · Chick survival

Introduction

Parent birds have to make a yearly decision on how much parental effort should be spent on the current breeding attempt, and how much should be saved for future reproduction (Clutton-Brock 1991). In addition to or, alternatively, in conjunction with this decision, parents must also allocate investment within the current brood (Martins and Wright 1993; Mock and Parker 1997). In times of food scarcity, being able to reduce the brood and allocate available resources into fewer young through preferentially provisioning larger, high-quality young may be beneficial (Lack 1954; Magrath 1989; Forbes 1991; Martins and Wright 1993; Mock and Parker 1997). Mechanisms for brood reduction may exist by which parents could assess the quality of each young (Lack 1954). However, during times of high food availability, all nestlings should be provisioned at equal rates (Amundsen and Stokland 1988; Forbes 1991, 1994).

Most species of gulls of the genus *Larus* lay a modal clutch of three eggs. In several gull species, the last-laid (c)-egg is significantly smaller than the two first (a- and b)-eggs (Parsons 1970; Reid 1987). The eggs generally hatch asynchronously, and the last-laid egg hatches 1.5–4 days later than the first two eggs (Paludan 1951; Parsons 1972). Parsons (1975) was the first to show a decreased probability of survival in the last-hatched herring gull chick and mortality in c-chicks was most pronounced shortly after hatching. Hatching asynchrony and small terminal egg size in gulls have been viewed as two adaptive characters, since they provide parents with a brood of chicks of different sizes, thereby facilitating facultative brood reduction in times of food

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scarcity (the brood reduction hypothesis; Lack 1954; Ricklefs 1965; Hébert and Barclay 1986). However, some studies (Pierotti and Bellrose 1986; Kilpi et al. 1996) have demonstrated that egg size may be constrained by poor feeding conditions.

Hatching asynchrony may also reduce wasteful competition between siblings (the sibling rivalry reduction hypothesis; Hamilton 1964; Hahn 1981). Thus a size difference between siblings should maintain a stable dominance hierarchy, which will reduce fighting between siblings and therefore lower the energetic costs for parents rearing their young (e.g., Hahn 1981). Several hypotheses are aimed at explaining the evolution of hatching asynchrony in birds, a good review of which can be found in Stoleson and Beissinger (1995).

The ultimate question is whether the normal degree of hatching asynchrony maximizes production of independent offspring in the long run compared to either more synchronous or asynchronous broods (Amundsen and Stokland 1988; Magrath 1989). Hébert and Barclay (1986) suggested that herring gull parents could maintain selective feeding of chicks shortly after hatching, cueing on the size asymmetry of the chicks at hatching. They stated that their study supported Lack's (1954) idea that brood reduction is facilitated through selective feeding of the largest and hence probably most fit young in the brood. Despite a large number of studies on large-sized gull species (Reid 1987), the reproductive benefits of hatching asynchrony in larids remains poorly understood (Bollinger 1994).

The aim of our study was to investigate parental care tactics in broods with different hatching patterns (synchrony/asynchrony). Our objectives were to determine if there was (1) an active brood reduction mechanism in herring gulls, and if so (2) whether this mechanism could be influenced by the manipulation of the sibling size hierarchy. Following Hébert and Barclay (1986), we predicted that increased asynchrony should lead to selective feeding of larger young and starvation of younger sibs. From the sibling rivalry reduction hypothesis, we predicted that experimentally increased synchrony should increase sibling competition and reduce breeding success compared to normal hatching asynchrony. We approached the question of the adaptiveness of hatching asynchrony in herring gulls using egg manipulations. Thus we did not focus on the possible effect of egg size on chick survival. A reason for not focusing on egg size effects was that we have no evidence for an egg-size-related third-chick disadvantage in our study colony (Kilpi et al. 1996).

Methods

Fieldwork was carried out from April to July 1993 on Storsundsharun, Hanko, southwest Finland (60° N 23° E). Storsundsharun is a small (1.5-ha) barren granite island with sparse patches of grass. The colony of herring gulls on this island has been fairly stable in size for the past 10 years and the annual number of breeding pairs ranges from 110 to 140 (unpublished data).

The entire colony at Storsundsharun was monitored daily during laying, and each nest was marked with a wooden stake at clutch initiation. Each egg in the sequence (a–b–c) was identified at laying and marked with a waterproof marker. Eggs were measured with calipers to the nearest 0.1 mm, and weighed with a Pesola spring balance to the nearest 1 g. Egg volume (cm³) was calculated from the equation:

$$\text{volume} = 0.000476 \times \text{length} \times \text{width}^2 \quad (\text{Harris 1964})$$

Egg laying of herring gulls is rather synchronous, and a clear peak laying period is usually found. Following Parsons (1976), who found that pairs laying in the peak period had the best reproductive success, we selected nests from this period for egg manipulations. Thus very early nests (the first 5 nests, 3.5% of all nests) and late nests (the 35 last nests, which comprised 25% of all nests) were omitted. The nests used in the experiment were initiated during a period of 17 days, between 13 and 30 April (median date was 22 April). The median laying date for the whole colony on Storsundsharun was April 24 ($n=139$ first nestings, relays not included). Because of the stability of the size of the colony, we expect most peak-laying pairs to be old and experienced breeders. Restricting the inclusion of nests to the experimental treatment to these "peak pairs" only should reduce bias resulting from including late-laying adults with little breeding experience (see Pugesek and Diem 1990).

Herring gulls generally begin effective, continuous incubation after the b-egg is laid (Paludan 1951), but may initiate incubation with the a-egg (Parsons 1972). The third c-egg normally hatches a day later than the b-egg, which hatches soon after the a-egg has hatched (Parsons 1975). Parental neglect just before hatching does not seem to affect the hatching success of the c-egg (Lee et al. 1993), and the hatching chick needs very little extra warming by a parent bird because it is warmed by siblings.

Our aim was to manipulate the normal hatching pattern by artificially inducing synchrony, in which all eggs in a clutch hatched within the same day (synchronous), and another group creating exaggerated asynchronous broods, where the c-egg hatched roughly 1 day later than the average natural hatching interval. In clutches designed to be synchronous, we removed both the a- and the b-egg as soon as the b-egg was laid, and replaced them with dummy eggs which were readily accepted. The a- and the b-egg were held in a moist storage room for 24–36 h at 12°C, and after this delay both eggs were returned to the nest. For asynchronous clutches, a- and b-eggs were left in the nest, but the c-egg was removed at laying, and held in a moist storage room for 24–36 h, at which time it was put back in the nest. Control clutches were created by removing the a-egg, replacing it with a dummy until the b-egg had been laid, at which time the a-egg was returned to the nest; the c-egg was not manipulated. This procedure included the removal process independently of c-egg laying. A fourth set of nests was unmanipulated, i.e., none of the eggs in the sequence was removed from the nest. All eggs in all nests were subject to marking, weighing, and measuring. Only one nest was destroyed following our manipulations, and the final set of nests ($n=103$) included was:

- (1) asynchronous experimental nests, henceforth called asynchronous (ASY, $n=19$)
- (2) synchronous experimental nests, henceforth called synchronous (SYN, $n=22$)
- (3) manipulated control nests, henceforth called control (CON, $n=21$)
- (4) unmanipulated control nests, henceforth called unmanipulated (UN, $n=41$)

For the treatment groups, we attempted to minimize differences that could affect the results. We randomized the allocation of nests each day to the treatment categories, and the final set of nests included in the study satisfied this requirement as far as the basic breeding parameters are concerned. There was no difference in laying date between treatment groups (Table 1), and the overall mean laying date for all nests analysed was April 21±4 (SD) days, ($n=85$ clutches). Territory size was similar among the groups, measured by nearest-neighbor distances (mean 4.0±0.3 m, $n=87$).

Table 1 Laying date (in April) of the a-egg, nearest-neighbor distances, total clutch volume, and relative size of the c-egg compared with the a-egg for the treatment groups (means \pm SD; *n* in parentheses). The table includes the result of a one-way ANOVA for differences between the treatment groups (log-transformed data for neighbor distances)

Treatment	Laying date	Nearest neighbor (m)	Clutch volume (cm ³)	c-egg volume (% of a-egg)
ASY	21 \pm 0.8 (19)	3.8 \pm 0.4 (19)	258 \pm 3.3 (15)	95 \pm 1.0 (15)
SYN	21 \pm 0.9 (18)	4.0 \pm 0.5 (19)	259 \pm 4.8 (18)	95 \pm 1.0 (19)
CON	23 \pm 0.8 (19)	3.2 \pm 0.3 (19)	257 \pm 4.2 (17)	97 \pm 1.0 (19)
UN	20 \pm 1.2 (28)	4.2 \pm 0.4 (31)	259 \pm 4.2 (21)	95 \pm 1.0 (22)
<i>F</i> -value	1.2	0.7	0.05	1.1
<i>df</i>	3,83	3,87	3,68	3,72
<i>P</i>	0.32	0.55	0.98	0.36

Table 2 Weights (g) and tarsus lengths (mm) of a-, b-, and c-chicks at hatching for each treatment group (mean \pm SD; number of individuals in parentheses). The table includes the result of a one-way ANOVA testing for differences between the treatment groups for each chick (for abbreviations see Methods)

Treatment	Chick weight			Tarsus length		
	a-chick	b-chick	c-chick	a-chick	b-chick	c-chick
ASY	69.2 \pm 2.5 (12)	69.0 \pm 1.4 (10)	65.5 \pm 1.2 (10)	28.1 \pm 0.3 (8)	28.9 \pm 0.2 (7)	28.0 \pm 0.3 (9)
SYN	68.6 \pm 1.4 (14)	69.7 \pm 1.8 (11)	68.8 \pm 1.9 (17)	29.1 \pm 0.5 (8)	28.2 \pm 0.3 (6)	28.9 \pm 0.2 (9)
CON	69.4 \pm 1.7 (13)	69.8 \pm 1.6 (14)	65.0 \pm 1.2 (16)	28.8 \pm 0.5 (9)	29.0 \pm 0.2 (8)	28.9 \pm 0.5 (10)
UN	69.6 \pm 2.5 (19)	69.0 \pm 1.4 (18)	66.2 \pm 1.1 (20)	28.9 \pm 0.3 (13)	28.4 \pm 0.5 (6)	28.4 \pm 0.3 (13)
<i>F</i> -value	0.10	0.01	1.42	0.82	1.18	1.04
<i>df</i>	3,54	3,49	3,59	3,34	3,23	3,39
<i>P</i>	0.92	0.99	0.24	0.49	0.34	0.38

The mean total clutch volume of three egg clutches was similar in all treatment groups (Table 1), but the size of a-, b- and c-eggs differed significantly [mean volumes, a-eggs=87.1 cm³, b-eggs=88.4 cm³, c-eggs=83.2 cm³; for c-eggs, blocked ANOVA, $F_{2,86}=8.42$, $P<0.0001$, Tukey (HSD) pairwise comparison of the group means]. However, the difference in volume between a- and c-eggs (which ranged from 3 to 5%), was similar in all treatment groups (Table 1).

Hatching was monitored daily. Chicks were marked with indelible marker pens on the egg-tooth at pipping, and on their down after hatching. This marking procedure made it possible to identify the chick hatching order. At an age of 5–7 days, they were marked with coloured PVC rings and steel bands. At hatching, chicks were weighed (with a Pesola balance to the nearest 1 g), and the length of the tarsus was measured (with calipers to the nearest 0.1 mm). The a- and b-chicks were weighed and measured again at the time of hatching of the c-chick, to establish the size hierarchy at hatching of the last chick.

Hatching mass did not differ between treatment groups (Table 2). In addition, tarsus length at hatching did not differ between treatments among chick categories (i.e., a-, b- or c-chicks; Table 2). Thus, chicks were of similar size and weight at hatching, though c-chicks were generally somewhat lighter than a- and b-chicks.

Subsequent behavioral observations were made only on broods that hatched all three chicks. These broods were monitored until the chicks reached an age of at least 30 days, and fledging success (~day 40; Paludan 1951; Kilpi 1990) was determined for as many pairs as possible. Behavior of the parents and chicks was observed from two hides, one on the island of Storsundsharun itself (L.H.) and the other on an adjacent small islet (M.K.), using binoculars ($\times 8$) and telescopes ($\times 30$). Scanning a fixed set of clearly visible territories, we tried to obtain as many observations as possible of feeding situations, recording the behavior of parents and chicks, and the outcome of each feeding in terms of which chick was fed. Since the first days of life are the most critical for survival (Parsons 1975; Kilpi 1990), we analyzed the feeding data separately for the first 10-day period.

Results

Results of the manipulations

There was a significant effect of manipulation on the hatching interval between the a- and the c-egg (one-way ANOVA, $F_{3,74}=12.2$, $P<0.0001$), so that in asynchronous broods, the c-egg hatched on average 2.6 days \pm 0.3 ($n=16$) later than the a-egg, whereas in synchronous broods the c-egg hatched 0.7 \pm 0.2 days ($n=16$) later than the a-egg. In unmanipulated control and manipulated control broods, this interval was 1.7 \pm 0.1 ($n=26$) and 1.3 \pm 0.2 ($n=19$), respectively. A post hoc Tukey (HSD) test indicated that both the asynchronous and synchronous groups differed from each other and from the control and unmanipulated groups, which were similar in hatching interval.

The experimental treatment also generated significant size difference effects between the a- and c-chick at the time of hatching of the c-chick, so that differences in weight were lowest in the synchronous group and highest in the asynchronous group (ANOVA, $F_{3,59}=6.3$, $P=0.0009$; Fig. 1). In asynchronous broods, a-chicks weighed on average almost 28 g more than c-chicks, while a-chicks in synchronous broods weighed only about 6 g more than c-chicks (Fig. 1). There was no difference in body mass between a- and b-chicks in the treatment groups (ANOVA, $F_{3,52}=0.29$, $P=0.83$). Size differences in tarsal length between a- and b-chicks versus c-chicks were also not significant, but showed a similar trend (ANOVA, $F_{3,37}=1.7$, $P=0.18$; Fig. 1). The in-

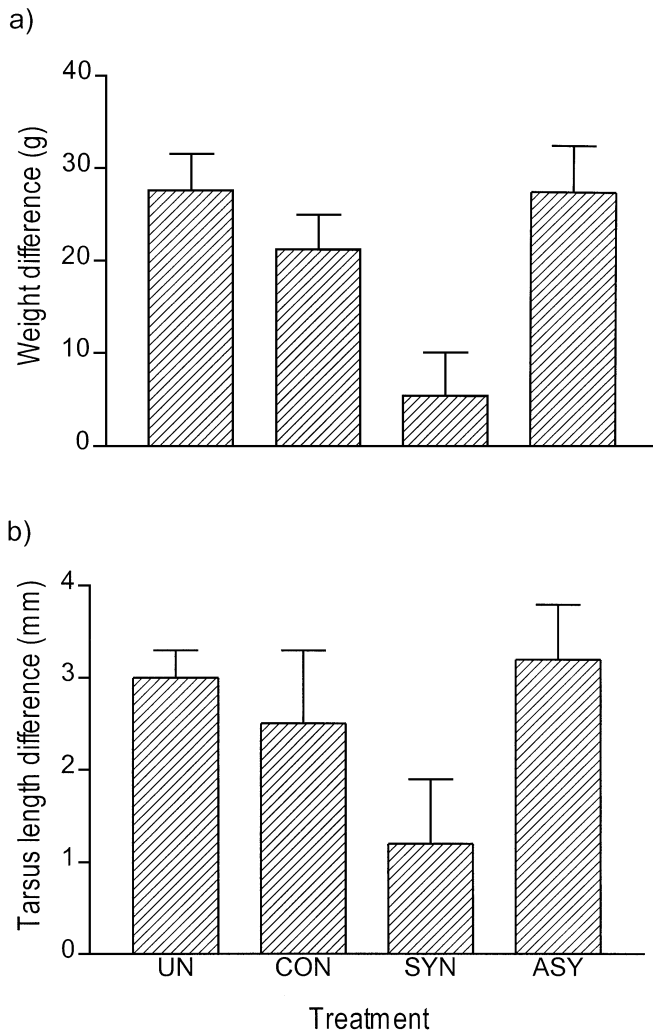


Fig. 1 Weight (a) and tarsus length (b) difference between a- and c-chicks in the treatment groups at the time of c-chick hatching (UN unmanipulated, CON control, SYN synchronous, ASY asynchronous). Means are given with 1 SE bar

creased hatching interval did not produce a significantly larger sibling size asymmetry in asynchronous broods than in unmanipulated control broods. Thus the egg manipulation experiment produced a marked contrast between the synchronous treatment and the other treatment groups. In contrast, size differences at hatching of the c-chick was not so pronounced in the asynchronous group (Fig. 1). In the manipulated control broods, some hatching synchrony seems to have been induced, because the birds were prevented from actively incubating (or merely sitting on) the a-egg.

Breeding success

Breeding success was generally very high. Of three-egg clutches that survived intact until hatching of the c-egg, asynchronous and control clutches had the highest hatching success [Kruskal-Wallis test, $H'=7.48$, $P=0.05$,

means (\pm SD, number of nests): ASY= 2.95 ± 0.23 , $n=19$; SYN= 2.55 ± 0.68 , $n=19$; CON= 2.90 ± 0.23 , $n=19$; UN= 2.65 ± 0.84 , $n=32$]. Of all the chicks that hatched into three-chick broods ($n=85$ pairs, 255 chicks), 73.8% fledged. When mortality of chicks was analyzed separately for the first 10-day period for all treatments together, a higher proportion of c-chicks (30%) died early in life compared to a- (13%) or b-chicks (16%; $\chi^2_2=8.9$, $P=0.01$). Thus in the first 10-day period, there was an overall lower survival rate of c-chicks compared to a- and b-chicks.

Similar numbers of chicks, however, survived to an age of 10 days in all treatment groups in nests hatching three young [Kruskal-Wallis test, $H'=1.80$, $P=0.78$, means (\pm SD, number of nests): ASY= 2.28 ± 0.75 , $n=18$; SYN= 2.53 ± 0.51 , $n=14$; CON= 2.33 ± 0.97 , $n=18$; UN= 2.32 ± 0.80 , $n=25$].

Of all pairs ($n=85$), 7.0% lost all chicks, 13% raised one, 31% raised two, and 49% of the pairs fledged all three young. Of all chicks that died ($n=66$), most did so before the age of 10 days ($n=50$, 76%). The mortality rate of chicks was 20% for chicks up to the age of 10 days and 8% after that age up to fledging at day 40. In 85 nests that hatched all three eggs, the precise identity of the chicks that fledged or perished was established. In these 85 nests, 64 a-chicks (75%), 65 b-chicks (76%) and 56 c-chicks (66%) successfully fledged, i.e., reached an age of 40 days. There were no significant differences in fledging success among the chick categories ($\chi^2_2=4.6$, $P=0.10$). Thus, there was no significant third-chick disadvantage at fledging.

Mean fledging success was similar in all treatment groups [Kruskal-Wallis test, $H'=3.50$, $P=0.32$, means (\pm SD, number of nests): ASY= 2.22 ± 0.81 , $n=18$; SYN= 2.14 ± 0.86 , $n=14$; $n=18$, CON= 2.33 ± 0.97 , $n=18$; UN= 1.87 ± 0.97 , $n=23$].

In the next analysis, we included data only for 73 nests for which we knew which chick died first if at least one perished. The mortality rate of a-, b-, and c-chicks up to an age of 10 days did not differ between treatment groups (a-chicks: $\chi^2_3=6.59$, $P=0.09$; b-chicks: $\chi^2_3=4.12$, $P=0.25$; c-chicks: $\chi^2_3=4.41$, $P=0.22$; Table 3).

Comparing survival for each chick category between treatments, there was high mortality (0.50) for c-chicks in the asynchronous group, and low mortality (0.0) for a-chicks in the synchronous group (Table 3). We further analyzed the frequency of death of the c-chick up to an age of 10 days against the frequency of death for a- and b-chicks combined to overcome small sample sizes. There were significant differences in survival among c-chicks compared to a- and b-chicks, both in the synchronous and in the asynchronous groups (Table 3). However, the survival rate of c-chicks in the synchronous group (35.7%) was not particularly low compared with the unmanipulated control group (34.8%) but, rather, the survival of a- and b-chicks in the synchronous group was relatively high (Table 3).

Table 3 The survival of chicks until age 10 days in the four treatment groups. This dataset includes only broods that hatched three chicks ($n=73$). The last two columns give the results from a χ^2 -test

Treatment	a-Chick		b-Chick		c-Chick		Test results	
	Dead	Alive	Dead	Alive	Dead	Alive	χ^2	P
ASY	3	15	1	17	9	9	7.92	0.005
SYN	0	14	1	13	5	9	5.47	0.019
CON	6	12	3	15	3	15	0.12	0.729
UN	3	20	6	17	8	15	1.18	0.277

($df=1$ in all cases) based on frequency, where a- and b-chicks have been combined and tested against the c-chicks

Causes of chick mortality

The most common cause of death was simply disappearance prior to the age of 10 days, accounting for 82% ($n=50$) of all losses (a-chicks=83%, b-chicks=92%, c-chicks=84%, $n=12$, 13 and 25 chicks, respectively). A few were killed by neighbors prior to an age of 10 days (a-chicks=17%, b-chicks=8%, c-chicks=8%) and two c-chicks (8%) were killed by weather-related accidents. Chicks that disappeared were most likely depredated by conspecifics, though this was rarely observed. We recorded one case of adoption of a non-family chick. Other attempts to recruit into strange broods by chicks must have been very rare, since we found no killed chicks (all chicks were marked) and no further broods with adoptees (see Pierotti and Murphy 1987).

However, after an age of 10 days most (69%, $n=16$) chicks perished due to conspecific killing. A few disappeared (two a-chicks, three b-chicks), two a-chicks were killed in territorial clashes, and three (43%) a-chicks, two (40%) b-chicks, and four (100%) c-chicks were killed and partly consumed by conspecifics.

Feeding behavior and chick behavior

Feeding chicks was generally a conspicuous behavior regardless of their age. The parent about to feed would call, and not start a feeding bout (i.e., start to regurgitate food on the ground) until all chicks were present ($n=113$ feedings). This was the general rule, and it did not matter which chick arrived first to the parent about to feed. Data from 27 territories of all treatment groups (pooled) during the first 10 days after hatching of the c-chick showed that all three chicks were fed in the majority of cases (88% of 113 feedings). Of 82 feedings at 23 territories in which all three chicks survived the 10-day period, 76 (93%) resulted in feeding of all three chicks. At 12 territories in which one or more chicks were lost, but at the time when all three were still alive, 24 out of 31 feedings (77%) resulted in all three chicks being fed. The frequency of territories where feeding of less than three chicks occurred (five in both groups) did not differ significantly between those that lost any chick prior to 10 days of age and those that did not lose any chick ($\chi^2_1=1.5$, $P=0.21$). The identity of the chick not fed was not established in most cases.

Of 96 feedings at 17 territories on which all three chicks still remained after the age of 10 days for the c-chick, only 14 (14%) involved less than three chicks being fed at those feedings. The identity of the chick not being fed was not established in enough cases to allow for more detailed analysis. We did not observe a single fight between chicks before an age of 10 days in any of the brood categories in the 27 territories over 113 feeding instances. It is possible that chicks may compete with each other outside feeding events, or use very subtle cues to establish a sibling hierarchy, but we have no data on such observations.

Discussion

Breeding success

The overall success of breeding pairs in our colony was markedly good (for a comparison among several colonies see Kilpi et al. 1996). A total of 76% of all hatched chicks fledged, indicating a very good feeding situation in the colony. We found no chick that had starved, and nearly half of all study pairs fledged all three young. We base this argument on our observations that gull chicks that have starved are never taken by conspecifics (see also Stanback and Koenig 1992).

The effect of egg size

Our results strongly suggest that there was no substantial disadvantage in being a c-chick in terms of survival to an age of 10 days in a natural, unmanipulated situation. This contrasts to several other studies on the herring gull, which have shown a considerable disadvantage for c-chicks (Parsons 1970, 1975; Davis 1975; Graves et al. 1984; Reid 1987).

The size difference we observed between the eggs within a clutch was among the smallest documented for this species (Pierotti 1982; Meathrel et al. 1987; Reid 1987). In fact, the egg quality was similar within clutches, assessed by dry weight analysis of yolk and albumen (Kilpi et al. 1996).

We found no significant differences in body mass and tarsus length at hatching. Pierotti and Bellrose (1986) found no effect of egg size on hatching weight or survival

al in the western gull *Larus occidentalis* when egg size within clutches was similar. We conclude that egg size did not have any effect on survival of c-chicks in our population. High survival costs seem to be associated with higher degrees of intra-clutch egg size asymmetry (9–11% smaller c-egg volume compared with a-eggs; Parsons 1975; Hébert and Barclay 1986; Kilpi et al. 1996).

Effect of synchrony

There was a significant effect of increased hatching asynchrony in manipulated, asynchronous broods. Thus, a larger hatching interval seemed to have a negative impact on early survival of c-chicks, but shortening the hatching interval did not seem to increase early survival of c-chicks relative to unmanipulated broods. Amundsen and Stokland (1988) also induced higher c-chick mortality in broods of the shag, *Phalacrocorax aristotelis*, when they experimentally doubled the normal asynchronous hatching pattern.

Hahn (1981) found that in laughing gulls, *L. atricilla*, natural asynchronous broods produced more fledglings than manipulated synchronous broods. In our case, synchronous manipulated broods on the whole produced as many chicks to fledging as did the other groups. Hébert and Barclay (1986) found that early survival in manipulated synchronous herring gull broods was enhanced, but later, differences were obscured. Thus, the only reasonably clear negative effect on the survival rate of c-chicks was found when asynchrony was increased.

Mortality in relation to age and size

Most of the mortality occurred in the early part of the nestling phase before an age of 10 days. This part of the nesting phase also seemed to be the period when directed mortality operates on c-chicks in asynchronous broods. Early nestling mortality has also been documented in other studies of herring gulls (Parsons 1970, 1975; Graves et al. 1984; Hébert and Barclay 1986; Kilpi 1989, 1990).

The brood reduction hypothesis and the sibling rivalry reduction hypothesis (Lack 1954; Hamilton 1964; Hahn 1981; Mock and Ploger 1987; Wiebe and Bortolotti 1994) both predict that brood reduction should come early in the nesting phase. The mortality of c-chicks in our study occurred early in life, which supports this prediction from both hypotheses.

A hierarchy among the chicks in a brood is a necessary condition for operation of the brood reduction hypothesis (Ricklefs 1965). Adaptive explanations consider age and size asymmetry as the primary cue for parents to identify the sibling hierarchy. These circumstances create the primary advantage for older sibs in the competition for food and the size hierarchy serves as a means for facilitating active brood reduction (Mock and Parker

1997). It should therefore be of importance to establish the magnitude of the size hierarchy in herring gulls. Few data exist on this point, but Parsons (1975) showed in his study on the herring gull that the average mass difference was 15% between the a- and c-chicks at the hatching time of the c-chick. In a natural situation, the difference between our a- and c-chicks was more pronounced, since a-chicks in the normally asynchronous (unmanipulated) broods weighed on average 29% more than c-chicks.

The mortality of c-chicks reported by Parsons (1975) was 59% within 7 days post-hatch. The c-chick mortality rate up to 10 days in our study was much lower, since only 35% of chicks in broods of natural hatching asynchrony died. Thus, although the size hierarchy was more marked in our study, c-chick mortality was lower than in Parson's (1975) study. In short, our study indicated no significant cost for smaller c-chicks in an unmanipulated natural situation in terms of sibling competition. Parents did not seem to feed any chick (a-, b-, or c-chicks) preferentially, since no chicks died of starvation in any of the groups we studied. Our results thus contradict the prediction that size hierarchies are important in brood reduction in large gulls.

Feeding behavior

There was an apparent cost for being a c-chick in the manipulated asynchronous broods. Hébert and Barclay (1986) found evidence for selective feeding of a- and b-chicks in normally asynchronous broods that they related to their superior ability to compete for food compared to c-chicks. Graves et al. (1984) proposed that c-chicks starved because they were not able to move as much as their siblings and parents selectively fed more mobile young. However, during our behavioral observations, feeding was never initiated until all chicks were present at the feeding spot, and parents even divided the food if chicks were unable to handle larger items rapidly. Unfortunately, our dataset is not sufficient to divide feeding behavior for separate analyses of different treatments. Therefore, we cannot entirely rule out the possibility that c-chicks from asynchronous broods were out-competed by their sibs. However, we imagine this to be unlikely, since even in this treatment group, no chick died of starvation. We propose that nestling mortality early in life was not an outcome of sibling competition, or of directed/selective feeding of larger chicks.

The sibling rivalry reduction hypothesis should render asynchrony advantageous independent of food supply (Hahn 1981), and has to be tested by comparing synchrony and asynchrony, i.e., if sibling fights increase in synchronous broods (Mock and Ploger 1987). Our data do not support the sibling rivalry reduction hypothesis. In large gulls, sibling aggression in general seems to be uncommon (R. Pierotti, personal communication). Our result was, however, obtained in a good year, and more studies in different feeding situations are needed.

Interestingly, Hébert and Barclay (1986) found that overall survival in experimental synchronous broods with slight size differences between chicks initially resulted in a higher rate of survival for the c-chick, at the expense of a- and b-chick survival rates. In our data, hatching into synchronous broods did not reduce survival of a- and b-chicks, and survival of c-chicks in synchronous broods was equal to that in broods with normal asynchrony. All groups produced an equal number of fledglings per nest.

Causes of nestling mortality and a mechanism favoring reduced asynchrony

The primary cause of nestling mortality in this study was disappearance of chicks, indicative of predation, most likely by conspecifics (Parsons 1971; Pierotti 1987; Kilpi 1989). We suggest that one of the primary reasons for chick loss was frequent kleptoparasitism on feedings by non-breeding herring gulls associated with the colony (Kilpi 1995). These attacks on feeding families led to some chicks being taken (we saw three cases, one of which ended fatally). This predation is different from that performed by specialist predators on chicks (Parsons 1971; Hario 1990), since kleptoparasites may pick up chicks unintentionally. As chicks are always fed openly, the risk that chicks will be taken by a predator will be reduced with development of motor skills, since it is essential to both handle food quickly and take shelter rapidly after a feeding. An inability to do this may be the cost of asynchrony to c-chicks. With large hatching asynchrony, the first two chicks will have had time to grow and develop motor skills. The feeding of the c-chick will then be hampered, not because it will not reach the feeding parent in time to feed (Graves et al. 1984), or because of sibling competition, but simply because it has difficulties in handling food and taking shelter rapidly.

We also wish to emphasize that only one chick from one brood was seen to be adopted by a non-related pair (Pierotti and Murphy 1987), so "running" does not seem to be a common cause of chick disappearance at an early age in our colony. Running, however, seems to be important in some other colonies (Pierotti and Murphy 1987).

Why is there asynchrony?

Parsons (1972) argued that herring gulls start incubation effectively even before the b-egg is laid. The reason for this must be the high risk of predation for unattended eggs, especially the first eggs (see Drent 1970). Thus a simple mechanical explanation for asynchrony is the need to start incubation before clutch completion, and asynchrony could be a consequence of minimizing risk of predation or increasing egg viability (Arnold et al. 1987; Bollinger et al. 1990). Support for the brood reduction hypothesis is very equivocal in studies on

gulls and terns (Reid 1987; Sydeman and Emslie 1992; Bollinger 1994). If there is strong selection for early incubation, some asynchrony is unavoidable, and no post-lay adaptive explanation is needed (Bollinger et al. 1990; Bollinger 1994).

Parsons (1972, 1976) proposed that the smaller c-egg size is an adaptation to reduce asynchrony, since c-eggs took a shorter time to incubate than larger a-eggs. In our study, c-eggs were quite similar in size to a- and b-eggs, and gained little in terms of incubation time. Thus, at least in a benign environment, herring gulls do not seem to reduce incubation time by laying small c-eggs (Kilpi et al. 1996).

Our results suggest that hatching asynchrony would most certainly generate a cost if it was larger than the normal asynchrony evolved in the herring gull. Our experimental treatment to induce more asynchrony had only slight effects on hatching hierarchy. Although manipulated asynchronous broods had an almost 1-day larger hatching span than unmanipulated broods, both body mass and tarsus length differences between a- and c-chicks were almost the same in these two treatments. The conclusion that can be drawn from this is that parents did not seem to feed the a- and the b-chick more in experimentally asynchronous broods. Thus, if parents are aware of large size differences among offspring, they may regulate the size hierarchy by feeding the a- and b-chick at a lower rate than they normally do if hatching is more synchronous (but see Lee et al. 1993). This remains to be tested.

The normal pattern of hatching asynchrony may probably be the best solution for herring gull breeding in good circumstances. Increased synchrony does not seem to improve production of young, but it does not lower it either. In a normal population, some pairs hatch their young synchronously in any case, and some pairs hatch their clutches very asynchronously (see MacRoberts and MacRoberts 1972).

Reid (1987) suggested that normal asynchrony in glaucous-winged gulls, *L. glaucescens*, is an adaptation for maximal growth under all circumstances. We suggest that herring gulls may also simply be doing their best to raise all three chicks in all situations, but early incubation needs and possible food constraints on laying birds which also affect hatching asynchrony sometimes cause unduly high c-chick mortality. Asynchronous hatching does not seem to be an adaptive strategy aiding brood reduction in this species.

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