

Chick growth and nest departure in Baltic Black Guillemots *Cepphus grylle*

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During apparently good food years, Black Guillemot *Cepphus grylle* chicks from the Gulf of Finland grew at a constant rate, showing the typical peak (asymptotic) weight and the subsequent weight recession prior to fledging. Single chicks fledged heavier than twins, but no differences emerged in departure age. Among twins, growth rate and fledging success were similar for A- and B-chicks. Chicks from artificially enlarged broods of three fledged lighter, had significantly shorter tarsus and a longer nest-rearing period than control broods of twins and singles, indicating food stress. The rate of parental feeding was positively correlated with brood size, but the increase was not proportional to brood size, so that chicks in larger broods received a smaller number of feedings per chick than those in smaller broods. The diet was similar among broods, containing 90% of Eelpout *Zoarces viviparus*. Despite the increase in provisioning effort, parents of enlarged broods did not discriminate between their own and alien offspring. Nest departure age was strongly affected by the combined effect of the developmental maturity of the chick's body dimensions and the depth of the nest cavity. In deep cavities, chicks needed to wait longer to attain the right body mass/wing length ratio for climbing out than in low ones. Because this study did not follow birds after fledging, immediate effects of lower body weight and shorter tarsus on survival cannot be assessed.

1. Introduction

In its circumpolar distribution, the Black Guillemot *Cepphus grylle* is an inshore-feeding alcid, typically breeding at low density in small colonies (e.g. Harris & Birkhead 1985). In the northern Baltic, it occurs throughout most of the zonal gradients of the archipelago (von Numers 1995), thus deviating from the strictly pelagic Razorbills *Alca torda* and Common Guillemots *Uria aalge*. It is a short-distance migrant, heading to the southern Baltic in August and returning upon the ice break-up in February-March. Juveniles leave

immediately after their (nocturnal) fledging and do not return to their natal sites until 1–2 years later (own obs.).

Unlike the other two Baltic alcids, the Black Guillemot adopts the semi-precocial fledging strategy, with a long nestling period and fledging weight close to that of adults (Sealy 1973). Although not fully capable of sustained flight, nest-departing young already have their juvenal feather growth completed when leaving the nest at the age of 30–40 days (Sealy 1973, Gaston 1985). This contrasts with the situation in Razorbills and murre, assigned as “intermediates” in their fledg-

ing strategy (Sealy 1973); their remigal growth only starts after the nest departure at the age of 15–30 days and at 15–35% of adult weight (Gaston 1985). Black Guillemot young are completely independent after fledging, whereas those of the intermediate species are escorted and cared for at sea by the male parent for another 70–85 days. During that period they reach the same asymptotic weight of about 90–95% of adult weight (Varoujean *et al.* 1979 on Common Murre, cited in Gaston 1985) that Black Guillemot chicks already attain in the nest.

In the Baltic, total failures of breeding have been reported during spells of cold sea water, in the event of food scarcity due to the (presumed) incatchability of the bottom-dwelling Eelpout *Zoarces viviparus*, and Butterfish *Pholis gunnellus*, the species' staple food (Bergman 1971, 1978). Chicks have died in nest, presumably through starvation. In several other areas, too, breeding success has varied widely (reviewed in Harris & Birkhead 1985, Barrett & Anker-Nilssen 1997). In normal food years, asymptotic weight is reached a few days prior to fledging, after which the weight recedes. In years without a pronounced asymptote, the mean weight curve either shows a continuous increase up to fledging, or a levelling off, and in both cases the mean fledging weight has been significantly lower (Ewins 1992). Several additional parameters have given further indications of failing food resources in those years (Asbirk 1979, Ewins 1992).

For fledging Black Guillemots, which depart alone and have no parental assistance during the prompt transition to independent feeding, the nutritional state and morphological development at nest departure are probably of prime importance (Gaston 1985, Hipfner & Gaston 1999). What factors are involved in the nest departure decision? Are the young themselves determining when to depart, or is it up to their parents? Is it possible to delineate the nutritional threshold that chicks need to attain to make a successful exit?

Feeding conditions for seabirds are difficult to measure, let alone to manipulate. One way to evaluate the food acquisition and the parents' ability to provide food is to add extra chicks into the modal-sized broods. This can set the stage for sibling competition, however, and immediate brood reduction. Last-chick disadvantage is considered

ecologically adaptive in the event of food scarcity (Lack 1947, 1954, Graves *et al.* 1984, Forbes 1994), even though its linkage to genuine starvation of the (smallest) chicks has hardly ever been proved (Davis & Quinn 1997, Hario & Rudbäck 1999). Siblings in Black Guillemot broods hatch at variable synchrony, ranging from 0 to 6 days and averaging from 0.5 to 1.5 days; roughly 50% of broods hatch within one day (Petersen 1981, Ewins 1992, Cook *et al.* 2000). Their mortality has varied broadly among studies (for reviews, see Harris & Birkhead 1985, Ewins 1989, 1992). Few previous works have addressed the nature of this mortality, whether accidental or biased towards the younger chick (but see Petersen 1981). Preferably, it ought to be accidental for brood enlargement experiments to show the role of food supplies on parents' ability to rear extra chicks.

This study was divided into two main sets. First, by monitoring the growth and fate of chicks in unmanipulated broods, I wanted to explore whether the mortality is accidental or biased. Second, I have added to the work load of the parents by artificially enlarging the brood size from two to three. When placing an alien hatchling of similar age into two-chick broods, I made the following assumptions:

1. Contrary to the situation in the cliff-nesting alcids, the cavity-nesting Black Guillemot parents do not recognise their own offspring (Lloyd 1977, Petersen 1981), thus being unable to discriminate between their own offspring and the alien nestling;
2. At every feeding instance only one fish is brought by the parent, and only one chick gets the fish and swallows it whole (Asbirk 1979), so the parents need to increase their feeding rate (readily observable in the field as an increased number of feeding flights), in order to get each chick satiated at a time, the extra chick included;
3. Because chicks depart alone and parents do not escort them, parents are able to continue provisioning for the remaining chick(s) in the nest after the first one has left.

My ultimate goal is to assess how chick departure decisions in Black Guillemot possibly reflect the species' divergent life history tactics among the Alcidae (e.g. Sealy 1973). The Alcidae are un-

usual in their wide range of inter-specific differences in nest departure strategy (Lack 1968). However, my approach is purely pragmatic; I do not aim to re-evaluate the recent debate over the evolutionary forces shaping this diversity (e.g. Ydenberg 1989, Gaston 1998, Hipfner & Gaston 1999).

2. Material and methods

2.1. Study area

The study was carried out at the Söderskär Game Research Station, central Gulf of Finland (60°10'N, 25°25'E), during 1998–2000. The area is a bird sanctuary in the sea zone 25 km southeast of Helsinki, consisting of 25 small islands and islets ranging in size from 0.2 to 6.3 ha. Most are treeless rocks, but the largest islands have boulder ridges and stands of aspen and spruce and extensive juniper cover. Black Guillemots prefer treeless islets of granite bedrock, fissured deeply with cracks and crevices, and fronted by jumbles of large boulders.

The Black Guillemot population in the area is about 200 pairs. This figure is based on counts of occupied nests, undertaken systematically from 1973 on, inclusive. Feral minks *Mustela vison* have had a pronounced effect on the population trends, but no minks appeared during the three study years. The study colony breeds in deep vertical fissures on an elevated granite rock, 2.9 ha in size. The fissures checker this spectacularly barren islet. It is the largest Black Guillemot colony in the sanctuary, consisting of 50–60 breeding pairs annually. Flooding (heavy rain and stormy wave action; there is no tide in the Baltic), and predation by Hooded Crows *Corvus corone cornix* are the main determinants of the colony size by readily spoiling breeding attempts in the openmost or otherwise exposed nest sites (own. obs.).

2.2. Field work procedures

In 1998 and 1999, I took a random sample of 18 nests and monitored the normal variation in chick growth and fledging age in them, separately for

one-chick broods (hereafter singles, $n = 13$) and for A- and B-chicks in two-chick broods (hereafter twins, $n = 12$; 11 nests failed). However, none of the single chicks originated from a genuine one-egg clutch, rather they started off with a twin and lost it, either in the egg stage ($n = 9$) or as a sibling ($n = 4$, losses occurred within 0–10 days from hatching). (Only one of the four true single-egg clutches hatched, but even that one was soon preyed upon, so it is not included in the growth data.)

The result of this preliminary investigation showed that twins were raised equally without any apparent last-chick disadvantage prevailing, so that a brood enlargement experiment could be feasible.

Each year, I checked the nest content in late May–early June, i.e. at the end of the laying period. Eggs were marked as soon as they were located and measured with a sliding caliper to the nearest 0.1 mm, and their volumes were calculated ($\text{length} \times \text{breadth}^2 \times 0.507$; Hoyt 1979). Visits on a daily basis (once a day) were started upon hatching, and continued (weather permitting) throughout the chick rearing period. Within a brood, I ranked chicks according to their hatching order; the first-hatching chick was then assigned as the A-chick. Sometimes both eggs were hatching on the same day; the pipping egg was then denoted A and the cracking egg, B.

In 2000, I created 5 artificial three-chick broods (hereafter triplets) by placing a foreign chick of similar age into two-chick broods around the hatching time. The nests were not the same that were monitored in 1998–99. The introduced young were from 0 to 3 day old and always of the same mass (within 3 g) as the original chicks in the nest (ANOVA, $F_{1,13} = 2.337$, $P = 0.149$). Their own hatching sequence (A or B) was not always known, but none of them was a single in its original nest. Within the foster brood, they were assigned as C-chicks. A further 10 nests (5 singles, 5 twins) were taken as controls.

Identity and age of the breeders were not known, but considering the fairly invariable clutch size of 2 in the nests monitored (47 nests with 2-egg clutches against 4 with 1-egg clutches in 1998–2000), the maturation effect on breeding performance is probably not important here. According to Asbirik (1979), mean clutch size in-

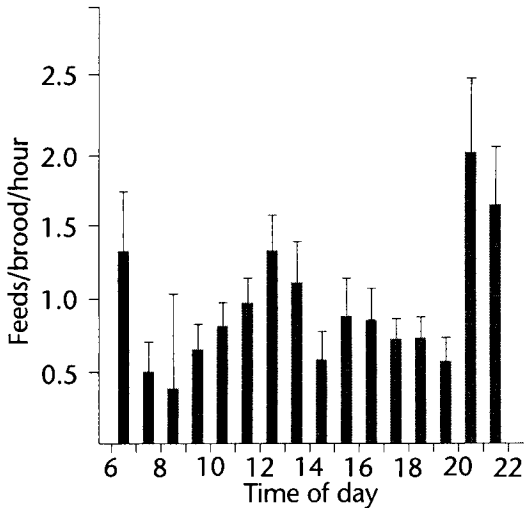


Fig.1. Diurnal rhythm of feeding rate of Black Guillemots at Söderskär in 1998–2000 (combined). Mean number of feedings/hour/brood + SE. $n = 108$ observation hours. No feedings occurred at 0600 and 2200 hours.

creases with parental age, so that the oldest age group (5–7 years in his study) always lays two eggs.

2.3. Nest site characteristics

Randomizing the nest site sample in relation to the colony centre (as commonly suggested for alcid studies, e.g. Gaston 1985) was dubious because of the highly scattered distribution of suitable nest cavities. No actual colony centre was discernible. However, I assessed the characteristics of the nest sites by measuring the chord length (in cm) of the cavity tunnel in the part, where a departing bird needed to make the highest climb at exit. As most nests were down deep in narrow fissures in the bedrock, this part was near-vertical in them, not horizontal. Being unable to take flight in the narrow crevice, the birds used their feet and claws and the bend of wing for climbing and jumping. This was seen several times from the hide at two nests that were situated in fissures beneath the hide site. Thus, I designated the measurement as “nest depth”, although it actually does not measure the total depth of the whole nest cavity, only the part where birds had to climb a near-vertical

hard surface to make their exit. This measurement ranged from 0 cm to 70 cm, median 30 cm, in the study sample ($n = 33$). Sites with no depth (0 cm) either had a horizontal entrance, or the tunnel walls sloped more than 30° from the vertical. The deepest vertical fissures in the study island are several metres deep and unsuitable for breeding. Every spring, several nest-prospecting adults were found dead in such fissures after they had failed to climb up again.

2.4. Measurements of birds

The characteristics measured were chick body weight and growth of the wings (all years), and growth of head and feet (in 2000). Measurements were taken on a daily basis, preferably in the afternoons, when most adults were out fishing and the disturbance effect was at its lowest. All the chicks were handled on every occasion.

Chicks were weighed to the nearest gram using Pesola spring balances. Wing length was taken as the maximum flattened chord (± 1.0 mm) using a stoppered ruler. Sliding calipers were used to measure (± 0.1 mm) the head length (the combined skull + bill length) and the tarsal length (from the notch of the intertarsal joint to the joint of the middle toe, with the toes bent back).

Measurements of adults stem from a sample of 53 adult birds swimming by the Söderskär colonies and caught for ringing purposes by means of a floating net in May. They were weighed and measured according to the methods described above (except that head length was not taken, only the bill length).

2.5. Feeding rates

Data on the food and feeding frequency of chicks were collected by direct observations of food-delivering parents during 29 days in 1998–2000. The observations (using $10\times$ binoculars) were done from a wooden hide overlooking the study colony. Altogether 12 nests were monitored (not simultaneously), 3 of which contained one chick, 3 had artificial triplets, and the remaining 6 nests had two-chick broods each. During a total of 108 hours (360 nest hours), 304 food deliveries were seen.

Observation times were rotated so that all of the daylight hours (between 0600 and 2300 h) were covered fairly equally (5–7 hours each).

The feeding frequency was not evenly distributed over the day, but tended to have three peaks: one in the morning, one at noon and one in late evening (Fig. 1). Also, the feeding rate varied according to chicks' age: it seemed to be highest during the period of the greatest mass increase of the chicks, i.e. around days 15–25. Since the age distribution of my data in relation to time of day was not equal over the entire monitoring period, I only used feeding results obtained during midday sessions (1100–1300 h) of 15- to 25-day-old broods. Feeding rate was calculated as the number of feedings per hour per chick. I compared the feeding rate between broods of different size (singles, twins, triplets).

No parent birds were lost from any of the nests monitored, as verified during the sessions in the hide.

2.6. Growth statistics

In the unmanipulated broods in 1998–99, there were no significant between-year differences in the proportions of single and two-chick broods (27% and 31% were singles, $\chi^2_1 = 0.091$, $P = 0.763$). Also, the weight and wing length curves of 1998 were equal to those of 1999, as was shown by screening the data on a computer as probability plots. Weight recession prior to fledging in unmanipulated broods was present in both 1998 and 1999, but not in 2000. The mean egg volumes for 1998–99 were also similar (t-test for matched pairs, $t_{39} = 0.340$, two-tailed $P = 0.735$) as well as the timing of hatching ($t_{39} = 0.176$, two-tailed $P = 0.862$). Thus, I have combined the two years' growth data and fitted them to a logistic growth model using Ricklefs' (1967) graphical method.

Since the asymptotic weight was not reached by the manipulated broods in 2000 (instead, they continued putting on weight up to fledging), I did not standardize their weight data by fitting them to an equation. Instead, I added a LOWESS smoother (locally weighted scatterplot smoother) to the data (Wilkinson *et al.* 1992). Smoothing does not presuppose the shape of the function. By

running along the x values it finds predicted values from a weighted average of nearby y values. This was applied to the control group in 2000 as well.

The daily growth rate was taken as the mean weight increment per day during the entire rearing period. The developmental maturity of the body dimensions (*sensu* Schew & Ricklefs 1998) at fledging was expressed as the ratio between the cube root of the body mass and the wing length. This ratio is assigned as the body condition index.

2.7. Fledging behaviour

In order to explore the nest departure decision of the nestlings, I performed a multiple linear regression analysis (backwards stepping; a minimum tolerance at 0.01) to determine which independent variables (nest depth, hatching date, body condition index, fledging wing length, fledging weight) were involved in the best-fitting model for predicting the nest departure decision, i.e. the fledging age (dependent variable). The consistency of the most powerful predictors was further tested with the Kendall coefficient of concordance statistic (Wilkinson *et al.* 1992).

Means quoted are arithmetic means, usually given ± 1 standard deviation. Tests are two-tailed, and significance is at the 0.05 level. Computations were achieved using the SYSTAT 5.0 software package.

3. Results

3.1. Natural variation in growth and nest departure

The growth of single chicks (b1 in Fig. 2) was slightly better than that of twins (b2A and b2B). However, none of the parameters in Table 1 were statistically different among groups except the fledging weight: single chicks differed from b2A (ANOVA, Tukey post hoc test; $P = 0.016$) and b2B ($P = 0.037$), which, on the other hand, did not differ from each other ($P = 0.937$). The overall breeding success (number of fledglings from the number of eggs) was 0.56 in 1998 and 0.43 in

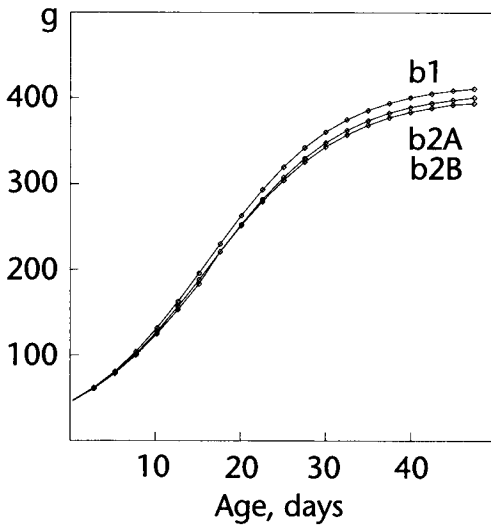


Fig. 2. The logistic growth curves of singles (b1) and twins (b2A and b2B) in Black Guillemot broods in 1998–99. Data presentation in Table 1.

1999. Egg losses amounted to 28% and 47% and chick losses to 23% and 19% in 1998 and 1999, respectively.

Among twins, the fledging result was similar (0.69) for both A- and B-chicks. Thus, chick mortality seemed to be accidental and not biased towards the younger chick. Loss of sibling led to a higher fledging mass of the remaining chick, but not to deviations in its age of nest departure (Table 1).

Despite the lack of asymptote, the daily mean growth rate of control broods in 2000 did not differ significantly from that of the unmanipulated broods in 1998–99 in terms of average weight increase per day (8.75 g/day against 8.95 and 10.53 in 1998 and 1999, respectively; $F_{2,113} = 0.36$, $P = 0.700$). The same applied to wing growth (3.25 mm/day against 3.66 and 3.67, $F_{2,108} = 0.32$, $P = 0.577$). The fledging weight of the controls (358 ± 35 , $n = 6$) was not significantly different from that of the twins in 1998–99 (377 ± 21 , $F_{1,20} = 2.25$, $P = 0.149$), though the sample sizes are small.

3.2. Variation in the manipulated broods

The predation by Hooded Crows was especially severe in 2000, curtailing the sample sizes of fledging young in control broods to 6 and in artificial triplets to 7. Fledging artificial triplets had significantly shorter tarsus ($F_{1,11} = 10.42$, $P = 0.008$) and retarded departure ($F_{1,11} = 3.65$, $P = 0.09$) compared to control broods (Fig. 3; summary statistics not presented). There was no difference in fledging weight, wing length and the head + bill length between the triplets and controls (F values less than 1.75, $P > 0.20$ in all cases).

The retarded mean departure of artificial triplets was an outcome of the remaining chicks staying in the nest for another 2–9 days after the first chick had left. During these additional days their

Table 1. Specific growth parameters of Black Guillemot chicks at Söderskär in 1998–99 (combined) according to brood size (b1 vs. b2) and hatching sequence (b2A vs. b2B). Adult weight at laying start and wing length given for comparison ($n = 50$ for both variables). One-way ANOVA has been used.

	b1 $n = 13$	b2A $n = 12$	b2B $n = 12$	
Asymptote (g)	420	410	405	
Growth rate (K)	0.164	0.160	0.156	
t_{10-90} (days)	26.7	27.5	28.2	
Adult body weight(g)	457 ± 43			
Hatching date	$24.VI \pm 5$	$25.VI \pm 8$	$26.VI \pm 8$	$F = 0.34$, $P = 0.718$
Egg volume (cm ³)	47.0 ± 2.1	46.8 ± 2.6	45.8 ± 2.8	$F = 0.74$, $P = 0.483$
Fledging weight (g)	407 ± 31	368 ± 31	373 ± 25	$F = 5.55$, $P = 0.010$
Fledging wing length (mm)	144 ± 3	143 ± 3	142 ± 3	$F = 1.11$, $P = 0.346$
Fledging age (days)	36.8 ± 1.4	36.6 ± 1.4	36.5 ± 1.2	$F = 0.10$, $P = 0.909$
Adult wing length(mm)	170 ± 6			

weight increased to approximate the weight of the first-departing chick (which in most cases was the B-chick; Fig. 3). A similar trend was seen in the head + bill length. The wing continued growing steadily, finally reaching the fledging length of the control group (145 mm in both groups, $P = 0.929$). In contrast, the tarsus growth reached its peak by about day 20 in all chicks and then stopped, showing no additional growth during the extra 2–9 nest-days of the slow-growing triplets.

3.3. Feeding rates

Parents feeding enlarged broods had suggestively higher feeding rates than those feeding normal broods (Table 2). However, mean feeding rate per chick was significantly higher in broods of singles (ANOVA, Tukey post hoc test $F_{40} = 0.46$, $P = 0.002$) and twins ($F_{40} = 0.31$, $P = 0.026$) than in broods of triplets. Although adults feeding enlarged broods were working harder, they could not feed each chick at the same rate as did parents of normal broods. Fish species brought to chicks were the same among the groups: triplets had 92.1% Eelpout ($n = 76$ fish identified), the rest being Herring/Sprat *Clupea harengus/sprattus* (5.3%) and Smelt *Osmerus eperlanus* (2.6%). The corresponding figures for normal broods were 88.0%, 5.2%, and 6.2% ($n = 210$), respectively. The proportion of Eelpout did not differ between the groups ($\chi^2 = 0.93$, $P = 0.335$). No apparent prey size adjustments among groups were detected, although I made no attempt to visually analyse fish size/mass distribution (fish delivered to small chicks were up to 5–10 cm long, but older chicks almost invariably got fish of 15–20 cm long).

3.4. Fledging behaviour

Multiple regression analysis indicated that body condition index was the most important independent variable affecting nest departure decision, i.e. the fledging age. However, as it was intercorrelated with fledging weight and wing length, I removed the latter ones from the model, after which the model was still significant ($F_{3,39} = 3.821$, $P = 0.017$). The three remaining variables (hatch-

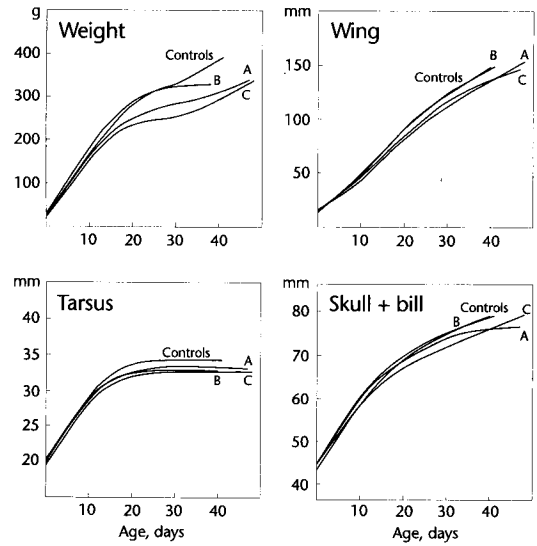


Fig. 3. Growth of different body components of A-, B- and C-chicks in the artificially enlarged broods, and the corresponding combined data of sibs in unmanipulated control broods in 2000. Lines give the smoothed curves of the growth rates.

ing time, nest depth, body condition index) were not intercorrelated, with hatching time having the least effect on the model (standard coefficient 0.034, $P = 0.813$). Consequently, the Kendall statistic was performed on fledging age, body condition index, and nest depth. The Kendall coefficient of concordance ($W = 0.751$, $P < 0.001$) indicated that there was a highly significant agreement between the ratings of these variables. I conclude that the nest departure decision (fledging age) was significantly affected by the combined effect of the nest's physical conditions (the nest

Table 2. Feeding rates in Black Guillemot broods of different size. Mean \pm SD ($n =$ number of sessions). One-way ANOVA gives the difference between the groups.

Feedings/hour/brood		Feedings/hour/chick	
Whole chick-rearing period		Days 15–24 only	
Singles	0.80 \pm 0.42 (37)	Singles	0.91 \pm 0.41 (20)
Twins	0.93 \pm 0.62 (43)	Twins	0.60 \pm 0.26 (15)
Triplets	1.36 \pm 0.71 (28)	Triplets	0.45 \pm 0.24 (10)
$F_{2,105} = 3.51$, $P = 0.035$		$F_{2,42} = 2.82$, $P = 0.071$	

depth) and the maturation of the chick's body dimensions (body condition index).

4. Discussion

4.1. Breeding success

The overall breeding success in the two unmanipulated seasons, 0.56 and 0.43 (as measured as the numbers of fledglings from the numbers of eggs laid), is lower than those documented in Shetland (0.60–0.70) and in northern Norway (0.64–0.73) during years of good feeding conditions (Ewins 1989, Barrett & Anker-Nilssen 1997), but higher than those from England (0.26), Canada (0.19–0.47) and Denmark (0.26–0.39) (Winn 1950, Cairns 1980, Asbirk 1979). In most studies, breeding success has been largely affected by predation, as was the case at Söderskär. In Iceland, however, there was very little predation and the breeding success in 1975–77 was very good, 0.68, 0.76 and 0.62, respectively (Petersen 1981). As sample sizes vary in favour of other studies, I will refrain from making a firm comparison between my results and those of other studies. However, I will evaluate the feeding conditions in my study years from other parameters (see later).

4.2. Last-chick disadvantage

There was no apparent last-chick disadvantage discernible among siblings in modal broods of two. This was seen in the cohesive growth rates, as well as in the equal survival of A- and B-chicks. The mean size of the A-egg did not differ from that of the B-egg; nor did their hatching dates differ significantly from each other. These can further be converted into the commonly used predictors of the last-chick fate, namely, the egg size asymmetry within a clutch (the percentage difference of the volume of the A-egg from the volume of the B-egg) and the hatching asynchrony (time interval between the hatching of the A-egg and B-egg). The mean values arrived at in this material, 1.7% (SD 3.2, $n = 25$, all three study years combined, enlarged broods excluded) and 1.2 days (SD 0.9, median 1.0, $n = 22$), are far below values considered critical, e.g. for the fate of

diseased C-chicks in gulls (6.2–8.8% and 4–5 days, Hario & Rudbäck 1996, 1999). Of course, hatching asynchrony and egg size asymmetry *per se* are not the reason for the last-chick disadvantage; they only measure the degree to which the last-layed egg is disproportional. These comparatively low values in Black Guillemots probably indicate a lesser degree of last-chick disadvantage as a whole (in the form of parental neglect; for sibling aggression see Cook *et al.* 2000).

However, no apparent last-chick disadvantage took place in the enlarged broods either, even though the hatching interval between the original sibs averaged 1.3 days (SD 0.8, median 1.5, $n = 10$) and the C-chick was detectably smaller than the A-chick for several days and probably easy to target then. The last-chick disadvantage is said to result from parents systematically expelling the chick(s) in which they have invested the least or which will require the most future investment (reviewed in Hario & Rudbäck 1999). 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.

Either the last-chick disadvantage does not normally exist among Black Guillemots (being inducible only experimentally, see Cook *et al.* 2000) or the food supplies were never sufficiently bad for creating pronounced “food scarcity”. Indeed, compared with other studies, Söderskär nestlings in 1998–99 were in good nutritional condition. The mean asymptotic weight (420 g) was about 90% of adult body weight (mean 457 g) of a sample of Söderskär birds of unknown breeding status (Table 1). The timing of the sampling, the latter part of May, indicates laying start. However, laying females in Denmark weighed 450 g, significantly more than incubating males and females (376 and 380 g, respectively) and even more than birds during the chick feeding period in a combined sample of both sexes (359 g; Asbirk 1979). Asbirk (1979) took the annual mean weight of incubating adults (374–378 g) as the reference value and got asymptotes of 105%, 95%, and 108% in the three study years. Adjusted to that, the Söderskär asymptote would approximate 112%, which is about the highest figure recorded

and probably an overestimate. But also at fledging, Söderskär chicks were heavier than their Icelandic counterparts (343–360 g, Petersen 1981) and Canadian ones (355–356 g, Cairns 1981), and similar to those in Denmark (361–377 g, Asbirk 1979) and Norway (379 g, Barrett & Anker-Nilssen 1997). This may be taken as a further indication of fairly benign feeding conditions at Söderskär in 1998–99.

4.3. Feeding rate in relation to brood size

Feeding rate was positively correlated with brood size, but the increase was not proportional to brood size, so that chicks in larger broods received a smaller number of feedings per chick per time unit than those in smaller broods, resulting in higher fledging weight of singles, but not in earlier nest departure.

These results are consistent with those of Ewins (1989, 1992) from Shetland. There, too, single chicks fledged significantly heavier than twins, and there was no indication of any genuine last-chick disadvantage in unmanipulated broods during the apparently good food years of 1983–84. At Söderskär, parents did not switch to higher-caloric food, but offered the same fish species and in the same proportions to enlarged broods and to normal broods (though the prey size distribution is not known, parental selection of smaller prey for triplets is highly improbable). This may simply stem from the narrow diet spectrum available in the central Gulf of Finland, which clearly deviates from the situation in areas of wider diversity (e.g. in arctic marine zones, Bradstreet & Brown 1985, and in Iceland, Petersen 1981).

Despite the greater parental effort and lack of discrimination, artificial triplets had low fledging weight and retarded departure compared to normal twins and singles. Apparently, parents were working at the upper range of their capacity, and the feeding conditions were not entirely good in 2000, although firm data are lacking. The lack of asymptotic weight in 2000 serves only as indirect evidence of food deficiencies, and the lower fledging weight, based on a small sample, was not statistically significant.

In contrast to the presumed food deficiencies experienced at Söderskär, the parents in Asbirk's

study (1979) in Denmark were able to feed all the three chicks in artificial triplets (5 cases) at an equal rate (0.46 fish per hour per chick) to twins (0.44) and singles (0.57), resulting in equal fledging weights among the groups (373, 361, and 377 g, respectively). No differences arose in fledging ages either, although Asbirk (1979) gives no details of fledging age variation within broods except that intervals of 1 and 2 days were common and the longest interval was 8 days.

Consistent with my results, 7 artificial triplets in Iceland had their nest departure age postponed by a mean of 7 days in 1975 and 5 days in 1976, their fledging weight averaging 297 g (SD 44) in 1975, i.e. nearly 50 g lower than that of normal twins and roughly 60 g lower than that of singles (Petersen 1981). As in the present study, enhanced feeding frequency of the parents was still not enough to maintain a constant ration for each chick; twins received ca. 30% fewer meals than singles. However, in 1976, there were no apparent differences in fledging weight among groups, and Petersen (1981) anticipated poorer feeding conditions in 1975.

I conclude that Black Guillemot parents at Söderskär could not, despite an increased effort, raise the feeding rate to meet the demands of enlarged broods, but that they, nevertheless, did not discriminate between nestlings. They prolonged the feeding period for as long as a chick was still in the nest. No adaptive brood reduction was discernible in the form of intentional killing of chicks through selective starvation. Chicks stayed in the nest until they attained a physiological state that allowed a successful departure.

4.4. Growth allocation and nest departure decision

Fledging age was strongly affected by the combined effect of nestlings' body dimensions (body condition index) and the nest cavity characteristics (nest depth). Apparently, there is a threshold in a bird's body dimensions that must be attained before a successful departure. Feet (and claws) are important, but I assumed that the cube root body mass/wing length ratio would better illustrate the maturation of a chick's body dimensions. This is because the constant growth of the feet

ceases already midway through the nestling period, whereas the wings continue to grow beyond the fledging period (in fact well into the first autumn–winter, Ewins 1992), being unaffected by daily oscillations in chicks' nutritional status (see also Gaston 1985).

Not surprisingly, the fledging length of the tarsus in the control group (34.1 ± 0.7 mm) was practically similar to that of adults (34.7 ± 1.3 , $n = 53$). The tarsus grew constantly and immediately after hatching, reaching the asymptote already around day 20 in all groups and independently of the chick's position within the brood. In contrast, head + bill length did not reach asymptotic values in any of the groups, and the size at fledging did not differ between triplets and controls.

Growth of head was of high priority in food-stressed Puffin *Fratercula arctica* chicks in the artificial feeding experiment by Øyan and Anker-Nilssen (1996). They concluded that preferential allocation of resources to the growth of the skull probably reflects the general need for a well-developed brain and nervous system and is therefore independent of body mass development (see also Schew & Ricklefs 1998). In their results, growth of the head had the highest priority in the event of food stress, followed by the wings and lastly the feet. This sequence may be similar in Black Guillemots, as judged from the fact that the tarsal length was the only body measurement that remained significantly smaller in artificial triplets compared to controls. Apparently, its size reflected the food stress up to day 20, after which the tarsus did not grow anymore, not even in the experimental triplets that stayed in the nest for an additional 2–9 days gaining weight and increasing their wing length and head + bill length to approximate that of controls.

Hence, the retarded nest departure of slow-growing triplets enabled nestlings to complete their growth of body dimensions so that they were able to climb up from the nest. The nest departure decision was therefore made by themselves and not by the food-providing parents. Apparently the chicks needed to attain a correct body mass/wing length ratio, which meant that chicks leaving from deep crevices had proportionately lower body mass in relation to wing length than those leaving from lower crevices. This resulted in the body

condition index being negatively correlated with departure age and therefore not intercorrelated with nest depth in the model explaining the timing of the nest departure decision (fledging age).

It seems plausible that nutritional state and morphological development are positively correlated with survival during the independent post-fledging period of Black Guillemot young, although the results from studies of several other alcids give no indication of that effect (Hedgren 1981, Harris 1982, Harris *et al.* 1992, but see Gaston 1997). This may be due to constantly benign environmental conditions in the low-latitude studies conducted so far. The Baltic Sea is probably one of the least extreme environments in terms of food acquisition by alcids as judged from the negligible between-year variation in guillemot chick growth here (Hedgren 1979, Hedgren & Linnman 1979). Even in the present study, induced food shortages might have been too brief to invoke anything more than temporarily slowed mass gain and possibly a permanent stunting of a character of lower maturation priority, viz. the tarsal length. However, both these traits can have prime effect on the immediate post-fledging survival. This effect was not studied at Söderskär, however, as there was no way to monitor the post-fledging young at sea.

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Selostus: Riskilän poikasten kasvu ja pesästä lähtö Suomenlahdella

Suotuisina ravintovuosina 1998–99 Söderskärin riskilän poikaset kasvoivat normaalivauhtia ja lähtivät pesästä keskimäärin 36 vrk:n iässä, ja niiden huippupaino, asymptootti, pari päivää ennen lähtöä oli noin 90 % aikuisen painosta (taulukko 1). Yhden poikasen pesyeissä lähtöpaino oli korkeampi kuin kahden poikasen pesyeissä (kuva 2), mutta lähtöikä oli sama. Kahden poikasen pesye-

eissä ei sisarusten välillä ollut eroa kasvussa ja pesästälähtöissä.

Ilmeisesti hieman huonompina ravintovuonna 2000 asymptoottipainoa ei saavutettu, vaan paino jatkoi hidasta nousuaan lähtöpäivään saakka, mutta jäi pienemmäksi kuin kahtena edellisellä vuonna. Keinotekoisien kolmosten (kahden poikasen peseysiin lisätiin yksi vieras kuoriutuja) pesästä lähtö venyi pitempään kuin verrokkipeseyneiden ja niiden paino jäi keskimäärin hieman alhaisemmaksi (kuva 3). Siiven pituudessa sekä pään + nokan pituudessa ei ollut eroa verrokkipeseysiin nähden, mutta nilkka oli merkittävästi lyhyempi. Myöhäisempi pesästä lähtö johtui siitä, että ensimmäisen poikasen lähdettyä jäljelle jääneet viipyivät pesässä vielä 2–9 päivää, jolloin paino vasta nousi esikoisen tasalle. Nilkan pituuskasvu päättyi kaikissa ryhmissä 20. elinviikon vaiheilla eikä enää jatkunut uudestaan niilläkään poikasilla, jotka viipyivät pesässä yliaikaa.

Emojen ruokintatahti oli pesyekokomanipulaatioissa korkeampi kuin verokkipesillä (taulukko 2). Ruokinta ei kuitenkaan kohonnut suorassa suhteessa poikasten lukumäärään, joten kolmost saivat vähemmän ruokintakertoja poikasta kohti kuin verrokkit. Ravinnosta 90 % oli kivinilkkää molemmissa ryhmissä (loppu silakkaa/kilohailia ja norssia). Keinotekoiset kolmost potivat ajoittaisista ravintostressistä, vaikkakaan niiden emot eivät suoranaisesti syrjineet peseytensä pienimpiä.

Päätöksen pesästä lähdöstä näyttivät tekevän poikaset itse. Siihen vaikuttivat poikasen siiven kehitysaste, ruumiinpaino sekä näiden ja pesäonkalon syvyyden yhteisvaikutus. Pystysuorista kallio-onkaloista ylös ponnistavien poikasten painon ja raajojen mittojen tulee olla oikeassa suhteessa, jotta poikanen pystyy kiipeämään halkeaman seinämällä sekä juoksemaan/pyrähtelemään rotkojen ja esteiden yli veteen. Pesästä lähtö tapahtui aina yöllä, ja poikasen tulee alusta alkaen pystyä omaehtoiseen ravinnon hankintaan, sillä emot eivät seuraa sitä merelle. Tämän itsenäistymisvaiheen arvellaan olevan siinä määrin kriittisen, ettei riskilän poikasella ole samantyyppistä "pelivaraa" kuntonsa ja kehittyneisyytensä osalta kuin ruokilla ja kiisloilla, joilla toinen emo seuraa poikasta merelle ja ruokkii sitä vielä pitkään. Ravinto-olot Itämeressä lienevät kuitenkin siinä määrin hyvät ja vakaat (= kivinilkan ja muiden limakalojen saanti), ettei poikasilla normaali-

listi ole vaikeuksia kasvussaan (riskiläkannat ovatkin vakaasti kasvaneet Suomessa). Poikaset eivät joutuneet tinkimään hermoston ja motoriikan osalta keskeisten elinten kehittymisestä, ja verrokkeja hitaampi painonnousu ilmentäne vain lieviä vaikeuksia rasvakerroksen kasvattamisessa. Sitä vastoin kasvukauden alussa lyhyemmäksi jäävä nilkka voi olla peruuttamaton ominaisuus, jota ei enää korjata istumalla pitempään pesässä emojen ruokittavana. Sen vaikutusta poikasen selviytyvyyteen pesästä lähdön jälkeen ei kuitenkaan tunneta.

References

- Asbirk, S. 1979: The adaptive significance of the reproductive pattern in the Black Guillemot, *Cepphus grylle*. — Vidensk. Meddr dansk naturh. Foren. Bind 141: 29–80.
- Barrett, R. T. & Anker-Nilssen, T. 1997: Egg-laying, chick growth and food of Black Guillemots *Cepphus grylle* in North Norway. — Fauna norv. Ser. C, Cinclus 20: 69–79.
- Bergman, G. 1971: Gryllteisten *Cepphus grylle* in einem Randgebiet: Nahrung, Brutresultat, Tagesrhythmus und Ansiedlung. — Commentat. Biol. 42. 26 pp.
- Bergman, G. 1978: Av näringsbrist förorsakade störningar i tejestens (tobisgrisslans) *Cepphus grylle* häckning. — Memoranda Soc. Fauna Flora Fennica 54: 31–32 (in Swedish with Finnish summary).
- Bradstreet, M. S. W. & Brown, R.G. B. 1985: Feeding ecology of the Atlantic Alcidae. — In: Nettleship, D. N. & Birkhead, T. R. (eds.), The Atlantic Alcidae: 263–318. Academic Press, London.
- Cairns, D. 1980: Nesting density, habitat structure and human disturbance as factors in Black Guillemot reproduction. — Wilson Bull. 92: 352–361.
- Cairns, D. 1981: Breeding, feeding, and chick growth of the Black Guillemot (*Cepphus grylle*) in southern Quebec. — Canadian Field-Naturalist 95: 312–318.
- Cook, M. I., Monaghan, P. & Burns, M. D. 2000: Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling black guillemots *Cepphus grylle*. — Behav. Ecol. 11: 282–287.
- Davis, J. & Quinn, J. S. 1997: Distribution of parental investment and sibling competition in the herring gull, *Larus argentatus*. — Behaviour 134: 961–974.
- Ewins, P. J. 1989: The breeding biology of Black Guillemots *Cepphus grylle* in Shetland. — Ibis 131: 507–520.
- Ewins, P. J. 1992: Growth of Black Guillemot *Cepphus grylle* chicks in Shetland in 1983–84. — Seabird 14: 3–14.
- Forbes, L. S. 1994: The good, the bad and the ugly: Lack's

- brood reduction hypothesis and experimental design. — *J. Avian Biol.* 25: 338–343.
- Gaston, A. J. 1985: Development of the young in the Atlantic Alcidae. — In: Nettleship, D. N. & Birkhead, T. R. (eds.), *The Atlantic Alcidae*: 319–354. Academic Press, London.
- Gaston, A. J. 1997: Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. — *Ibis* 139: 673–678.
- Gaston, A. J. 1998: Modeling departure strategies in auks. — *Auk* 115: 798–800.
- Graves, J., Whiten, A. & Henzi, P. 1984: Why does the herring gull lay three eggs? — *Anim. Behav.* 32: 798–805.
- Hario, M. & Rudbäck, E. 1996: High frequency of chick diseases in nominate Lesser Black-backed Gulls *Larus f. fuscus* in the Gulf of Finland. — *Ornis Fenn.* 73: 69–77.
- Hario, M. & Rudbäck, E. 1999: Dying in the midst of plenty — the third-chick fate in nominate Lesser Black-backed Gulls *Larus f. fuscus*. — *Ornis Fenn.* 76: 71–77.
- Harris, M. P. 1982: Seasonal variation in fledging weight of the Puffin *Fratercula arctica*. — *Ibis* 124:100–103.
- Harris, M. P. & Birkhead, T. R. 1985: Breeding ecology of Atlantic Alcidae. — In: Nettleship, D. N. & Birkhead, T. R. (eds.), *The Atlantic Alcidae*: 155–204. Academic Press, London.
- Harris, M. P., Halley, D. J. & Wanless, S. 1992: The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. — *Ibis* 134: 335–339.
- Hedgren, S. 1979: Seasonal variation in fledging weight of Guillemots *Uria aalge*. — *Ibis* 121: 356–361.
- Hedgren, S. 1981: Effects of fledging weight and time of fledging on survival of Guillemot *Uria aalge* chicks. — *Ornis Scand.* 12: 51–54.
- Hedgren, S. & Linnman, Å. 1979: Growth of Guillemot *Uria aalge* chicks in relation to time of hatching. — *Ornis Scand.* 10: 29–36.
- Hipfner, M. J. & Gaston, T. 1999: Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. — *Ecology* 80: 587–596.
- Hoyt, D. F. 1979: Practical methods of estimating volume and fresh weight of bird eggs. — *Auk* 96: 73–77.
- Lack, D. 1947: The significance of clutch size. — *Ibis* 89: 302–352.
- Lack, D. 1954: *The natural regulation of animal numbers*. — Oxford, Clarendon Press. 343 pp.
- Lack, D. 1968: *Ecological adaptations for breeding in birds*. — Methuen, London. 409 pp.
- Lloyd, C. S. 1977: The ability of the Razorbill *Alca torda* to raise an additional chick to fledging. — *Ornis Scand.* 8: 155–159.
- von Numers, M. 1995: Distribution, numbers and ecological gradients of birds breeding on small islands in the Archipelago Sea, SW Finland. — *Acta Zool. Fennica* 197: 1–127.
- Petersen, A. 1981: *Breeding biology and feeding ecology of Black Guillemots*. — D. Phil. thesis, Univ. Oxford. 378 pp.
- Ricklefs, R. E. 1967: A graphical method of fitting equations to growth curves. — *Ecology* 48: 978–983.
- Schew, W. A. & Ricklefs, R. E. 1998: Developmental plasticity. — In: Starck, J. M. & Ricklefs, R. E. (eds.), *Avian growth and development: evolution within the altricial-precocial spectrum*: 288–304. Oxford University Press, New York.
- Sealy, S. G. 1973: Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. — *Ornis Scand.* 4: 113–121.
- Varoujean, D. H., Sanders, S. D., Graybill, M. R. & Spear, L. 1979: Aspects of common murre breeding biology. — *Pacific Seabird Group Bulletin* 6: 28.
- Wilkinson, L., Hill, M., Welna, J. P. & Birkenbeuel, G. K. 1992: *Systat for Windows: Statistics, Version 5 Edition*. — Evanston, IL: SYSTAT, Inc., 1992. 750 pp.
- Winn, H. E. 1950: *The Black Guillemots of Kent Island, Bay of Fundy*. — *Auk* 67: 477–485.
- Ydenberg, R. C. 1989: Growth-mortality trade-offs and the evolution of juvenile life histories in alcidae. — *Ecology* 70: 1494–1506.
- Øyan, H. S. & Anker-Nilssen, T. 1996: Allocation of growth in food-stressed Atlantic Puffin chicks. — *Auk* 113: 830–841.