

Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling black guillemots *Cepphus grylle*

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Siblings in a diversity of species are facultatively aggressive, yet the proximate control of the aggressive response and the ecological conditions selecting for such systems are poorly understood. In this study, we investigated the effects of food amount (food amount hypothesis) and competitive asymmetry on sibling aggression in black guillemot broods. Parental provisioning rates were experimentally manipulated in broods comprising a range of hatching intervals over a 12-h period. Aggression became evident only after parental provisioning rates were experimentally reduced. When parental provisioning resumed, adults did not increase their feeding rate to compensate for the induced food deficit, and the result of sibling rivalry was a change in the allocation of parental deliveries from one of equality to one in favor of the dominant chick. Food-deprived chicks from synchronous broods were more aggressive than those from asynchronous broods, suggesting that one benefit of hatching asynchrony in the black guillemot is to establish an efficient competitive hierarchy among siblings which minimizes the need for costly aggressive interactions. On the following day, sibling aggression ceased, and chicks regained an equal share of parental feeds. Our results provide the first evidence that short-term food shortage per se acts as an initial trigger for aggression and also show that the aggressive response is complicated by factors associated with hatching and laying order. *Key words*: black guillemot, *Cepphus grylle*, competitive asymmetry, facultative aggression, hatching asynchrony, provisioning, sibling rivalry. [*Behav Ecol* 11: 282–287 (2000)]

Systems in which sibling competition is manifest through overt aggression provide quantifiable measures of selfish behavior among close genetic relatives (Drummond and Garcia Chavelas, 1989). In addition, they offer the opportunity to elucidate the underlying proximate and ultimate factors driving sibling conflict and brood reduction (Mock and Parker, 1997). It is widely recognized that, in bird species where sibling aggression is facultative, the level of parental provisioning may be an important proximate cue. This putative relationship between provisioning and aggression has been formalized in the “food amount hypothesis” (Mock et al., 1987). According to this hypothesis, dominant siblings become more aggressive during periods of food shortage, thereby obtaining a disproportionate share of total available parental resources. If this is reversible, when favorable food supplies resume, aggression rates should return to baseline levels.

Despite the logic underlying these predictions, only two studies have experimentally demonstrated a proximate link between parental provisioning level and sibling aggression in birds (blue-footed boobies *Sula nebouxii*: Drummond and Garcia Chavelas, 1989; ospreys *Pandion haliaetus*: Machmer and Ydenberg, 1998). This paucity of experimental data makes it difficult to identify the ecological conditions that favor the evolution of the facultative response and of the particular environmental cues that may trigger it.

The functional significance of facultative sibling aggression is likely to depend on the magnitude of competitive asymmetry between siblings. In most species the competitive dy-

namics of a brood are largely determined by the timing of the onset of incubation in relation to egg-laying patterns (Amundsen and Stokland, 1988; Fujioka, 1985; Hahn, 1981; Magrath, 1992; Slagsvold et al., 1984). For many avian species that begin incubation before their clutch is completed, the degree of hatching spread is relatively constant between individuals. Hence, the opportunity to investigate the extent to which variation in the degree of competitive asymmetry within broods influences the pattern of sibling aggression is limited. However, in some species, the degree of hatching spread varies considerably between pairs, but few studies have investigated the level of sibling aggression associated with this variation.

In this study we examined sibling aggression in broods of the black guillemot (*Cepphus grylle*), a seabird species that exhibits considerable interpair diversity in the degree of hatching asynchrony (in our study population, ranging between 0 and 6 days; Cook et al., unpublished data). Although the majority of breeding pairs lay a two-egg clutch, black guillemots differ markedly in the inter-egg interval and in the timing of the onset of incubation in relation to egg laying (Petersen, 1981). The resulting variation in hatching patterns creates a wide range of size disparities between siblings. Here we report the results of an experiment investigating the response of black guillemot siblings to reduced parental food deliveries. The study had two objectives: first, to determine experimentally whether food amount is a proximate cue for sibling aggression, and second, to investigate how the pattern of aggression varies in relation to the highly variable degree of competitive asymmetry within broods.

METHODS

General

Data presented here were collected on the Holm of Papa Westray, Orkney, Scotland (59°22' N, 2°53' W). The Holm is ap-

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proximately 0.8×0.3 km, uninhabited by humans, and free from mammalian predators. Adult black guillemots breed in loose aggregations, nesting predominantly within boulder caves on rocky shores but also among cracks in cliffs and occasionally in vacated rabbit burrows. Because direct observations of behavior inside the nest cavity were not possible, we developed a system of miniature charge couple device (CCD) cameras with infrared LED illuminators linked to closed-circuit television (CCTV) and Sony-walkman video recorders to monitor chick behavioral interactions and parental provisioning. The colony comprised approximately 65 breeding pairs of black guillemots in 1997, from which we collected a total of 252 h of observations, made on 20 nests.

Suitable nest sites (i.e., those that were in range of the CCTV system and safely accessible) were located and the camera system installed before egg laying began. To determine egg-laying dates, we checked each nest daily during the period of low adult attendance (approximately 1200–1700 h; Cairns, 1987) and marked each egg according to laying order. On completion of the clutch, nests were undisturbed until a few days before estimated a-egg hatching date (eggs are incubated for about 28 days; Ewins, 1986), whereupon daily nest checking was resumed to determine hatching dates and hatching interval.

Within each brood, siblings were referred to as either the A- or B-chick. This was related to hatching order in asynchronous broods (A-chick hatches first in broods where the hatching interval ≥ 1 day; mean hatching interval: $1.64 \text{ days} \pm 0.24$ SE, range 1–3 days) and to tarsus length in synchronous broods (A-chick being the larger in broods where chicks hatch on the same day). The A-chick in each brood was marked on the head with a small streak of correcting fluid (Tipp-Ex) to facilitate sibling identification. This mark looked similar to fecal spots that regularly appeared on A- and B-chicks. To determine sibling size disparity for each brood, we weighed and measured all chicks on the day before behavioral observations. We measured chick body mass to the nearest 1 g using an Ohaus 200-g electronic balance or 500-g spring-balance, depending on chick mass, and measured tarsus length to the nearest 0.1 mm using Vernier calipers. All broods were measured at approximately the same time of day (between 1100 and 1300 h), and no chick measurements were taken during the food reduction experiment.

Food reduction experiment

We recorded nestling behavior in response to changing food availability between 2 and 31 July 1997. To control for potential age-related differences in agonistic behavior, observations were confined to broods with A-chicks aged 6–12 days (by which age chicks were capable of thermoregulation, were rarely brooded by their parents, and sibling aggression rates were highest; Cook et al., unpublished data). Although this age category represents a potential age disparity of up to 6 days between broods, it represents only a small proportion of the nestling period (black guillemots fledge between 30 and 40 days; Ewins, 1986; Harris and Birkhead, 1985; Petersen, 1981), and significant age-related changes in behavior over this age range are unlikely. Incidentally, A-chick age did not differ significantly between treatment groups (experimental broods: mean age = $9.0 \text{ days} \pm 0.57$ SE, $n = 15$; control broods: mean age = $8.8 \text{ days} \pm 1.16$ SE, $n = 5$; Mann-Whitney test, $U = 33.5$, $p = .72$), nor between synchronous and asynchronous experimental broods (synchronous broods: mean age = $9.0 \text{ days} \pm 1.47$ SE, $n = 4$; asynchronous broods: mean age = $9.0 \text{ days} \pm 0.62$ SE, $n = 11$; Mann-Whitney test, $U = 21$, $p = .90$). On reaching the appropriate age, designated

broods were randomly assigned to either the experimental or control treatment.

Each of 15 experimental nests was observed continuously for 12 h, partitioned into three periods, during which parental provisioning rates were manipulated. During period 1 (3 h, from 0600 to 0900), broods were observed under conditions of natural parental provisioning. During period 2 (6 h, from 0900 to 1500), parental provisioning was prevented in the experimental nests by placing an adult scaring device—either balloons with painted eyes or a fiberglass great black-backed gull—near the entrance of the nest and in view of the returning adult. Deployment of a scaring device outside the nest provided a noninvasive means of preventing parents from entering the nest chamber and provisioning the young without directly affecting chick behavior. At the start of period 3, the final period lasting from 1500 to 1800 h, we removed the scaring device, and parental provisioning quickly resumed (a feed was recorded at all nests within 30 min). We also observed five control nests, at which parental deliveries remained undisturbed, over the same 12-h period as experimental broods.

A team of four observers recorded behaviors from the monitors during the 12-h period, two pairs each working a continuous 6-h shift. During any one 12-h period, four nests were observed directly from the monitors, and two were recorded using the Sony-walkman video recorders and analyzed later. To ensure inter-observer consistency, observers independently analyzed the same sample of video footage (9 h), both at the start and end of the season. In both cases, behavioral scoring and recordings by the four observers was identical for 89% and 96% of the behavioral events, respectively. We attempted to control for possible effects of hatch date and daily variations in weather condition by observing, during any one 12-h period, experimental nests comprising a range of hatching intervals (from 0–3 days) and at least one control nest.

Preliminary studies during the 1996 breeding season revealed that aggression was employed exclusively by the larger sibling and usually involved several bouts of violent pecking and tussling of the smaller chick, usually about the nape of the neck, face, or back of the head. The recipient chick tended to assume a submissive posture and rarely attempted to retaliate or evade its attacking sibling. Submission was characterized by crouching as low as possible, and any attempt to raise the head was often met with further bouts of attacks. B-chicks frequently died in unmanipulated nests where parental provisioning was poor, although the cause of death, whether directly through aggression or indirectly through starvation, could not be established. [For the 1996 and 1997 breeding seasons combined, 21 B-chicks from 69 broods (30.4%) succumbed to nonpredation-related fatalities, whereas only 7 A-chicks (10.1%) suffered a similar fate.] For the 1997 study, specified behavioral events were recorded directly onto data sheets using the focal-animal sampling technique (Altmann, 1977). We quantified aggression in terms of the number of attacks (violent pecks, jabs, or grasps) that each chick directed at its sibling, each individual attack being recorded as a discrete event. Adult black guillemots transport a single whole prey item to the nest crosswise in their bills, and on entering the nest chamber food allocation is determined largely by scramble competition; the sibling that first reaches the provisioning parent generally receives the prey item. Thus, only one sibling is fed during each parental delivery. A record was made of the total number of parental deliveries to each nest and the recipient chick of each feed.

To investigate the potential reversibility of the aggressive response, we observed five experimental nests that had exhibited high rates of aggression for 3 h on the day following the manipulation of parental provisioning rates.

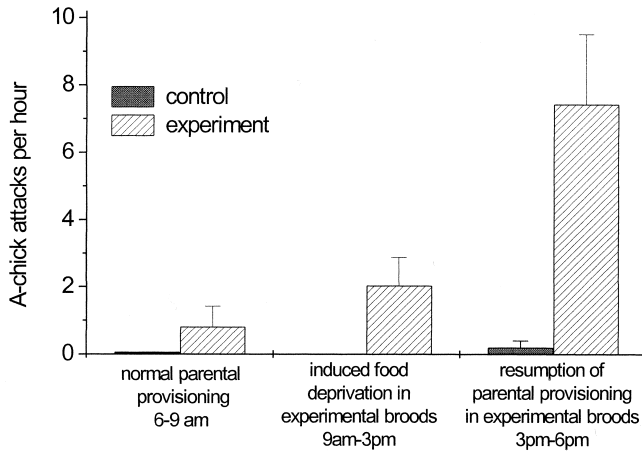


Figure 1
Mean (\pm SE) number of black guillemot A-chick attacks per hour during each period of the 12-h observation in control ($n = 5$) and experimental ($n = 15$) broods.

Our experimental design was such that periods of stress for the chick were short and well within the range experienced under natural conditions.

Statistical analysis

We used parametric statistics when data met the parametric assumptions of normality, homoscedasticity, and in the case of repeated measures ANOVA, sphericity. Where sphericity was not met, we used the Greenhouse-Geisser adjustment, whereby both the numerator and denominator degrees of freedom were multiplied by ϵ (Zar, 1996; SPSS for Windows release 7); F values were then calculated using the adjusted degrees of freedom. Appropriate nonparametric statistics were applied where these assumptions were not met. For proportional data, we used an arcsine square-root transformation to normalize data. Normality was tested for using the Kolmogorov-Smirnov goodness-of-fit test, and all probabilities given are two tailed. Analyses were conducted using SPSS for Windows release 7, and all tests were as described by Zar (1996).

RESULTS

Control broods

Siblings generally behaved nonaggressively in the control broods throughout the entire 12-h observation period: no B-chick aggression was observed and, although a very low rate of A-chick aggression (attacks/h) was noted in two of five control broods, no change in A-chick aggression rate occurred from period 1 through period 3 (repeated measures ANOVA, effect of period: $F_{2,8} = 0.64$, $p = .55$; Figure 1). Hence, we detected no evidence of any diurnal pattern of aggression in black guillemot A-chicks. Likewise, parental delivery rates (feeds/h) at each control nest did not differ significantly during the three periods (repeated measures ANOVA, effect of period: $F_{2,8} = 1.92$, $p = .21$; Figure 2), with A-chicks receiving similar proportions of parental deliveries during each period (repeated measures ANOVA, effect of period: $F_{2,8} = 0.10$, $p = .90$; Figure 3).

Experimental broods

Period before food restriction

During the period before food restriction (period 1), parental delivery rates (Mann-Whitney test, $U_{15,5} = 24$, $p = .24$; Figure

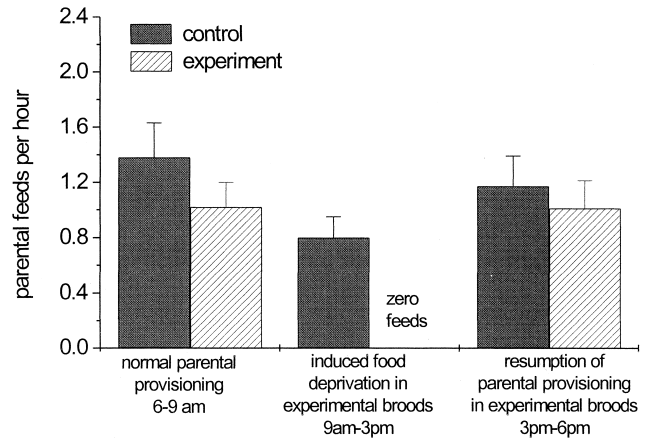


Figure 2
Mean (\pm SE) number of black guillemot parental feeds per hour during each period of the 12-h observation in control ($n = 5$) and experimental ($n = 15$) broods.

2) and the proportion of deliveries received by each sibling in experimental nests (Mann-Whitney test, $U_{15,5} = 36$, $p = .89$; Figure 3) did not differ significantly from those of the control group. In addition, sibling aggression rates in experimental broods were extremely low during period 1, and no significant difference in attack rate was evident between treatment groups during this period (Mann-Whitney test, $U_{15,5} = 35$, $p = .77$; Figure 1).

Food deprivation period and post food deprivation period

Aggression. Sibling aggression became evident in experimental broods after the restriction of parental food deliveries, occurring in 13 of 15 broods during periods 2 and 3. No attempt was made by parents to interfere in sibling aggression during period 3, despite the presence of one or more adults at the nest during a number of aggressive bouts. Aggression was performed exclusively by A-chicks in 10 broods, exclusively by the B-chick in one brood, and by both siblings in two broods. In the case where the B-chick was agonistic, bouts were of relatively short duration and did not elicit a submissive response from the A-chick. Thus, because A-chicks were the predominant aggressors and never subordinate, aggression was analyzed with respect to these chicks. Figure 1 shows the mean number of attacks on siblings in the experimental group dur-

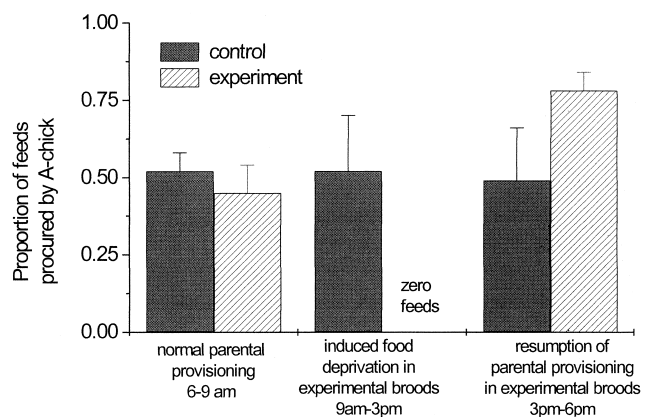


Figure 3
Mean (\pm SE) proportion of feeds procured by black guillemot A-chicks during each period of the 12-h observation in control ($n = 5$) and experimental ($n = 15$) broods.

ing the three periods. During periods 2 and 3, A-chicks in experimental broods became aggressive, significantly increasing their attack frequency relative to period 1 (repeated measures ANOVA, effect period: $F_{1,3,18,3} = 7.67$, $p = .008$, with Greenhouse-Geisser adjustment). A-chick aggression rates in experimental broods were significantly higher than in control broods during both period 2 (Mann-Whitney test, $U_{15,5} = 17.50$, $p = .049$) and period 3 (Mann-Whitney test, $U_{15,5} = 10.0$, $p = .014$).

Parental provisioning

If hunger is the underlying proximate cause of aggression, the food amount hypothesis predicts that A-chick aggression will be associated with a corresponding increase in the share of available parental deliveries. Figure 3 shows the mean proportion of feeds received by siblings during each period. As in control nests, parental delivery rates to each experimental nest remained constant between period 1 and period 3 (paired t test, $t = 0.21$, $n = 15$, $p = .84$; Figure 2). The mean proportion received by each chick in experimental nests was similar during period 1 (A-chick, 0.45; B-chick, 0.55; Wilcoxon matched-pairs signed-rank test, $z = 0.05$, $n = 15$, $p = .96$). However, after food deprivation, A-chicks received relatively more feeds than their sibling did (A-chick, 0.75; B-chick, 0.25; Wilcoxon matched-pairs signed-rank test, $z = -2.87$, $n = 15$, $p = .004$; Figure 3), with the proportion received significantly increasing from period 1 to period 3 (paired t test, $t = -2.26$, $n = 12$, $p = .045$; Figure 3). Parental delivery rates were similar between treatment groups during period 3 (Mann-Whitney test, $U_{15,5} = 28.0$, $p = .41$), with the effect that the total amount of food received by the experimental broods during the 12-h period was lower than that of control broods.

Competitive asymmetry and aggression

As expected, size disparity between siblings was significantly higher in asynchronous than in synchronous broods, both in terms of mass (Mann-Whitney test, $U_{11,4} = 7.0$, $p = .049$) and tarsus length (Mann-Whitney test, $U_{10,4} = 3.0$, $p = .016$). Figure 4 shows the relationship among hatching interval, sibling mass disparity, and the mean number of A-chick attacks/h in experimental broods in the periods during and after food deprivation (i.e., periods 2 and 3). Hatching interval had a significant effect on the level of aggression within the nest, with A-chicks from synchronously hatching broods attacking their sibling considerably more often than those from asynchronous broods (Mann-Whitney test, $U_{4,11} = 6.0$, $p = .036$). Aggression rates of A-chicks in asynchronous broods during periods 2 and 3 were significantly higher than during period 1 (Wilcoxon matched-pairs signed-rank test, $z = -2.24$, $n = 11$, $p = .025$). In synchronous broods, aggression rates increased in all broods during periods 2 and 3 relative to period 1, but the small sample size precluded statistical testing (Figure 4).

Reversibility

An implicit assumption of the food amount hypothesis is the reversibility of the system; aggression should decrease to baseline levels on resumption of satiation, with siblings thereafter receiving an equal share of resources. Behavioral data obtained from five experimental nests the day after manipulation supported this assumption: aggression rates in these nests declined considerably, with sibling interactions being largely passive, and the previous skew in the distribution of parental food deliveries toward the A-chick returned to unity. Both sibling aggression rates (mean attacks/h: period 1, 1.88 ± 1.80 SE; after period 1: 0.36 ± 0.23 SE; Wilcoxon matched-pairs signed-rank test, $z = -0.54$, $n = 5$, $p = .60$) and the allocation of parental food deliveries (mean proportion of feeds re-

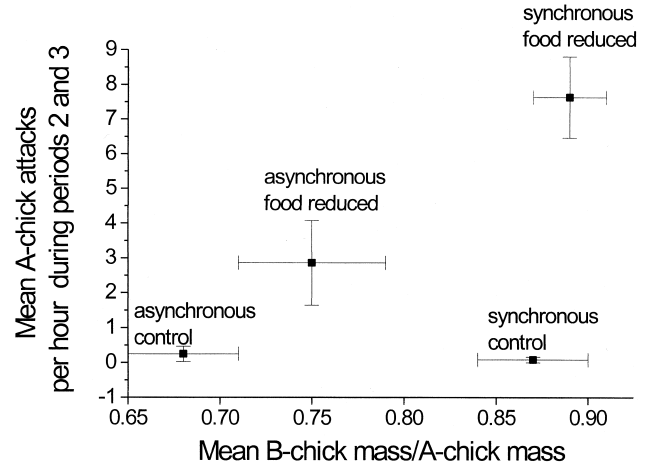


Figure 4

Mean (\pm SE) total number of black guillemot A-chick attacks during periods 2 and 3 for synchronous ($n = 4$) and asynchronous broods ($n = 11$) in the experimental group, in relation to mean (\pm SE) sibling size disparity (expressed as mass of B-chick divided by mass of A-chick).

ceived by A-chick during period 1: 0.52 ± 0.036 SE; proportion of feeds received by A-chick after period 1: 0.50 ± 0.045 SE; Wilcoxon matched-pairs signed-rank test, $z = -0.37$, $n = 5$, $p = .72$), did not differ significantly from those recorded during period 1 of the experiment.

DISCUSSION

A-chick aggression in black guillemot broods was elevated only after parental provisioning rates were experimentally reduced. When parental provisioning resumed, adults did not adjust their feeding rate in response to changes in their offsprings' requirements, and the consequence of the intersibling aggression was a skew in the distribution of food received by siblings in favor of the dominant A-chick. Moreover, the system was reversible; on the day after manipulations, A-chick aggression rates returned to pre-food-deprived levels, and B-chicks regained an equal share of parental feeds. Thus, by mediating aggression in accordance with changing nutritional requirements, A-chicks ensured a feeding advantage over their sibling when parental provisioning rates were reduced.

A further factor influencing aggression in food-deprived broods was competitive asymmetry. Food-deprived A-chicks from synchronous broods were significantly more aggressive than those from asynchronous broods, suggesting that fights were more common in situations where the dominance status of siblings was ambiguous. These results are consistent with game theoretical approaches to animal contests (Maynard Smith and Parker, 1976) and support empirical studies which showed that artificially synchronized broods were more aggressive than natural asynchronous broods (Fujioka, 1985; Mock and Ploger, 1987; Osorno and Drummond, 1995). An alternative explanation for higher aggression rates in synchronous broods is related to the relative ability of siblings to respond to and sequester parental feeds. Parents return to the entrance of the nest chamber with a single prey item, prompting a scramble competition among siblings, and the successful chick receives the entire delivery. In asynchronous broods, older, more developed chicks might gain greater access to parental deliveries without the need for aggressive domination by virtue of superior locomotory skills. In synchronous broods, however, because both chicks are competitively similar in feeding scambles, the A-chick is likely to gain a greater proportion

of feeds by being aggressive. Although a multitude of hypotheses exist for the functional significance of hatching asynchrony (see Stoleson and Beissinger, 1995, for review) the results of our experiment suggest that one benefit of asynchrony in the black guillemot is to establish an efficient competitive hierarchy among siblings which minimizes the need for costly aggressive interactions (see Hahn, 1981; Hamilton, 1964). Such a system is also believed to operate in certain species of Ardeidae (Fujioka, 1985; Mock and Ploger, 1987), Sulidae (Anderson, 1989; Osorno and Drummond, 1995), and various raptors (Forbes, 1991; Machmer and Ydenberg, 1998; Viñuela, 1999; Wiebe, 1995; Wiebe and Bortolotti, 1994). However, Amundsen and Slagsvold (1991) point out that although moderate degrees of asynchrony could be adaptive, relatively large hatching intervals have the potential to promote unnecessary brood reduction, regardless of environmental conditions. For example, in the facultatively siblicidal black kite, moderate hatching asynchrony reduces sibling rivalry, yet younger chicks in broods with extreme asymmetries suffered the highest mortality rate and the most serious injuries (Viñuela, 1999). In the current study, broods with hatching intervals >3 days were unavailable for experimental manipulation, and thus the effect of extreme asymmetry on black guillemot sibling aggression has yet to be established.

The influence of competitive asymmetry on black guillemot nestling aggression suggests that the proximate response is controlled not only by food shortage but also by factors associated with laying and hatching order. The observed aggressive disparities among siblings, particularly those in synchronously hatching broods where size and age differences were negligible, imply an inherent capacity for aggression. Schwabl (1993) postulated that such within-brood variation may be a consequence of differential concentrations of maternal hormones secreted into the yolk during egg maturation. Indeed, a correlation between sibling social rank and testosterone content of the eggs from which they hatched has been demonstrated in some avian species (Schwabl, 1993, 1996; Schwabl et al., 1997). It is also possible that nestlings are visually sensitive to size asymmetry within the brood and base the decision to elevate aggression rates on the competitive ability of their sibling. Clearly, further data are required to establish a comprehensive picture of the proximate causal pathway of sibling aggression. Nonetheless, our evidence that aggression in the black guillemot increases in both synchronous and asynchronous broods when food is reduced strongly implicates food shortage as the initial and primary stimulus for the aggressive response.

A fundamental prerequisite for the evolution of sibling rivalry is the existence of a resource deficit that has fitness consequences for the offspring (in terms of maintenance, growth, and survival) and ultimately creates a competitive environment within the brood (Mock and Parker, 1997; based on inclusive fitness theory, Hamilton, 1964). However, the use of overt aggression between competing sibs has been documented in relatively few avian taxa (Mock and Parker, 1997), with most species relying on passive forms of dominance such as relative begging vigor or the monopolization of favorable positions within the nest (Bengtsson and Rydén, 1981; Gottlander, 1987; Stamps et al., 1989). The reason for this dearth of violent interactions is straightforward: sibling aggression is costly (in terms of energy expenditure, risk of injury, etc.), and for selection to favor aggression in competitive avian sibships, the long-term fitness benefits of fighting must outweigh the potential costs (Lamey and Mock, 1991). In this context, it might be argued that since the induced deprivation in the current study was short-term, the resulting effects were potentially reversible and thus had little effect on chick fitness. Therefore, comparable short-term effects under natural con-

ditions (e.g., due to weather conditions or kleptoparasitism) would not provide the selection pressure necessary for the evolution of an expensive aggressive response. Nonetheless, several lines of circumstantial evidence suggest that food amount may be an important ultimate cause of black guillemot sibling aggression. For example, the fact that nonpredation-related mortality rates are considerably higher in the first 2 weeks after hatching than during the remainder of the nestling period [17 of 21 B-chicks (80.9%) that suffered nonpredation-related mortality in 1996 and 1997 died before 12 days], implies that even short-term reductions in parental delivery rates may confer significant fitness consequences for young black guillemot chicks. Moreover, sibling aggression in black guillemots is highest in young broods (Cook et al., unpublished data), peaking between 4 and 12 days after hatching and declining rapidly with age thereafter. This close association between chick age, aggression, and mortality lends some support to the notion that significant fitness benefits may be accrued through fighting.

An additional factor that may determine the cost effectiveness of sibling aggression is the defensibility of the food delivered to the brood. Mock (1984, 1985) formalized the relationship between prey defensibility and aggression with the "prey-size hypothesis," positing that sibling aggression is more likely to be selected for in species where parentally delivered food arrives in monopolizable, small units. Parent black guillemots deliver a single, economically defensible prey item to the brood, with the result that during any one delivery, only a single chick is fed. Such monopolizability in black guillemot broods may allow fighting to be relatively cost efficient because submissiveness on behalf of the B-chick can significantly skew parental investment toward the A-chick.

For food amount per se to be a reliable proximate cue in the regulation of aggression, short-term parental provisioning rates must be predictable; that is, periods of inadequate current provisioning must correlate with future food shortages that affect brood fitness (Mock and Parker, 1997; Mock et al., 1987). If this assumption is not met, then either a more reliable proximate cue or, if no forecast of future costs can be made, a strategy of obligate aggression should be used (Mock and Parker, 1997, 1998). In contrast to the Atlantic puffin (*Fratercula arctica*), where provisioning rates were found to vary in response to offspring requirement (Cook and Hamer, 1997; Harris, 1983), we observed no increase in black guillemot provisioning rate to compensate for the lack of prey supplied during the experimental period of induced food restriction (Figure 2). Thus, under natural conditions, it is possible that adults supply food to the brood at an intrinsically set rate, and any reduction in provisioning rate (e.g., due to inclement weather conditions) may not be subsequently compensated for. The implication that inflexible provisioning rates are a selective pressure in the evolution of the agonistic response is therefore supported by our observation that periods of poor provisioning appeared to be associated with a predictable forthcoming energy deficit to the brood, regardless of future feeding conditions. However, the time scale over which parental responses to chick need were recorded may have been too short to detect any compensatory increase in provisioning. Furthermore, although the rate of food supply to black guillemot broods did not appear to be regulated by adjustments in feeding frequency, it is possible (although unlikely) that regulation occurred through prey size adjustments. Further studies are required to verify the inflexible nature of parental provisioning and to examine in greater detail the relationship between current and future food supply.

Two previous studies have experimentally demonstrated a proximate link between food supply and aggression in nestling birds, yet important differences exist between the three

study species in the mechanism regulating hunger-mediated aggression. Drummond and Garcia Chavelas (1989) revealed that dominant blue-footed booby nestlings exhibit a baseline level of aggression regardless of current provisioning rates, increasing attack frequencies in response to their nutritional condition rather than to short-term fluctuations in food supply. In contrast, aggression rates in ospreys, although influenced by hunger, are largely determined by the degree of size asymmetry within the brood (Machmer and Ydenberg, 1998). In black guillemots, although aggression levels were higher in synchronous broods, sibling aggression increased in response to food deprivation regardless of the degree of hatching spread. This study is therefore the first to demonstrate that short-term food reduction per se can function as an initial trigger for aggression among avian siblings. More studies on other species are necessary so that further inter-specific comparisons of the aggressive response can be made. By identifying the ecological conditions and biological features that favor these different strategies, a greater understanding of the evolution of sibling aggression will be achieved.

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