



Sustained increase in food supplies reduces broodmate aggression in black-legged kittiwakes

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The amount of food ingested by chicks has often been suggested as being the main proximate factor controlling broodmate aggression in facultatively siblicidal species. Although several experiments have demonstrated that short-term food deprivation causes a temporary increase in aggression, no study has, to our knowledge, experimentally manipulated overall food supplies and considered long-term effects on chick behaviour and life history traits. We provided supplemental food to breeding pairs of black-legged kittiwakes, *Rissa tridactyla*, over an entire breeding season and compared the aggressive behaviour of their chicks with that of chicks of control pairs. Control A-chicks (first to hatch) showed more frequent and intense aggression than their experimental counterparts. Furthermore, the more A-chicks begged and the lower their growth rate the more aggressive they were. The consequences of increased aggression for B-chicks (second to hatch) were lower begging rate, lower growth rate and lower survival. We thus provide evidence that a sustained increase in food availability affects broodmate aggression and chick survival at the nest and we discuss the various proximate and ultimate causes involved in the evolution of broodmate aggression.

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In many animal taxa, parents routinely create more zygotes than they can ordinarily afford to raise (Lack 1947, 1954; Mock & Parker 1998). Such offspring overproduction is widespread in many bird species, generating sibling rivalry and, in many cases, leading to the death of the last-hatched chick. To explain the production of the extra egg, Lack (1947, 1954) formulated the 'brood reduction hypothesis'. Birds produce a brood with the maximum number of chicks they can successfully fledge during years of good food availability. During poorer years, broods are reduced to match the amount of food available. Brood reduction

provides a mechanism that adjusts brood size to food resources during the nestling period.

In most taxa, brood reduction occurs through differential starvation. In a minority of species, brood reduction is caused by siblicide which occurs through aggression of a chick towards a younger sibling leading to its death or ejection from the nest. At the proximate level, food is also assumed to be the resource driving nestling conflict. Mock (1987) formalized this idea with the 'food amount hypothesis' (FAH) according to which sibling aggression is negatively correlated with the quantity of food the aggressor ingests. This hypothesis is largely supported by field studies (osprey, *Pandion haliaetus*, western grebe, *Aechmophorus occidentalis*, cattle egret, *Bubulcus ibis*; reviewed in Mock & Parker 1998) and has now been experimentally confirmed for several species that show facultative siblicidal brood reduction (osprey: Machmer & Ydenberg 1998; blue-footed booby, *Sula nebouxii*: Drummond & Chavelas 1989; black guillemot, *Cephus grille*: Cook et al. 2000; black-legged kittiwake, *Rissa tridactyla*: Irons 1992; reviewed in Drummond 2001b).

To test the FAH, these studies manipulated the amount of food ingested by depriving chicks of food. With this approach, however, one cannot discount the possibility that aggression increased in

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response to frustration rather than to a reduction in quantity of food. Furthermore, the methods used for manipulating food intake were intrusive, such as tapes or wires to prevent food ingestion (Drummond & Chavelas 1989; Irons 1992; delaMora et al. 1996; Rodriguez Girones et al. 1996), removing the chick from the nest (Machmer & Ydenberg 1998), or placing a model predator to prevent parental access to the nest (Cook et al. 2000), which may lead to substantial biases in chick behaviour, thus potentially affecting the measurement of the chicks' aggressive response.

In this study, we tested the FAH by experimentally varying food supplies over a whole season and studying its impact on sibling aggression and brood reduction. This was done by differentially feeding parents raising two chicks. This protocol allowed us to investigate the effect of increasing food availability on broodmate aggression. Food supplementation was sustained over the whole breeding season in a nonintrusive manner, thus avoiding all biases caused by manipulation, as we neither handled and manipulated chicks nor disturbed their parents.

We first examined the effect of the feeding treatment on parental feeding of chicks as well as on A-chick (first hatched chick) begging behaviour, growth and survival. Second, we considered the effect of food supply on two parameters of chick aggressive behaviour: frequency and intensity of aggression. Third, we investigated whether variables likely to be affected by the food supply such as begging rate, feeding rate and growth explained such aggressive behaviour. Last, we studied the consequences of A-chick aggression on B-chick (second-hatched chick) begging and feeding behaviour, growth and survival.

METHODS

Study Population

The behavioural study was conducted from 23 June to 17 July 2005, in a colony of black-legged kittiwakes nesting on an abandoned U.S. Air Force radar tower on Middleton Island (59° 26'N, 146° 20'W), Gulf of Alaska. Artificial nest sites created on the upper walls were viewable from inside the tower as each nest site was fitted with a sliding pane (26 × 30 cm) of one-way mirror glass. This set-up enabled us to monitor breeders and chicks easily (from a distance of 20 cm, for more details see photographs in Gill & Hatch 2002).

Experimental Procedure

The amount of food available to parents was manipulated as part of a large-scale food supplementation programme examining the effects of food supply on breeding parameters in kittiwakes (see Gill & Hatch 2002; Gill et al. 2002). Breeding pairs were divided into two groups: Fed pairs were provided with supplemental food whereas Unfed pairs were not. Pairs of both groups were clustered (to avoid food stealing between neighbouring pairs), each treatment occupying alternating walls of the 12-walled polygonal-shaped tower. Pacific populations of kittiwakes have been experiencing a food shortage since the mid-1970s. On Middleton Island for instance, the colony has suffered total or near-total breeding failure in 15 of 17 years between 1983 and 1999, annual productivity averaging only 0.06 chicks per nest built (Gill & Hatch 2002). This productivity reaches 1.26 when birds are given extra food (Gill & Hatch 2002), suggesting that reproductive failure in Pacific populations is at least partially explained by an insufficient food supply. This particular context thus allowed us to study the effects of parental food provisioning on chick behaviour by increasing food supplies rather than decreasing them.

Supplemental feeding started on 4 May, on average 27.22 ± 0.61 days before the laying of the first egg, and stopped on 15 August (103 days of provisioning) when most chicks had fledged. The Fed pairs were given capelin, *Mallotus villosus* (average individual mass: 25 g), a high-quality natural prey of kittiwakes, bought frozen and thawed to ambient temperature before feeding. Feeding sessions occurred three times daily (at 0900, 1300 and 1700 hours). During each feeding session, fish were proffered singly through a plastic tube passing through the wall at each nest site. Feeding continued until satiation of the parent(s) present at the nest. Experimental chicks did not feed from the tube during the period considered in this study and were fed normally (by regurgitation) by the parents throughout the day.

We checked all nest sites twice daily (0900 and 1700 hours) to record events such as hatching or chick mortality. Chicks were weighed and measured every 5 days from hatching to fledging (ca. 40 days old). Body mass was measured to the nearest gram using an electronic scale and wing was measured with a stop-rule. Chicks were marked on the head with a nontoxic marker to identify their rank (red for A-chicks, blue for B-chicks).

Experiments were carried out in accordance with applicable United States law under permits from the U.S. Fish and Wildlife Service and State of Alaska (Department of Fish and Game) and approved by the French committee of animal ethics.

Behavioural Observations

Observations were carried out on nests containing two chicks in one or several 1 h sessions per day (from 1000 to 1830 hours) with 30 min devoted to nests of each treatment. As most aggressive behaviour in chicks occurs in the first 20 days after hatching (see Fig. 3 in the Results), chick behaviour was recorded from the day the second chick hatched until it was 20 days old, if it had not died or been displaced before then.

Behaviour of chicks was monitored for a total of 1620 min with an average of 924 ± 88 s/nest ($N = 105$). In the Fed treatment, 41 nests were monitored for a total of 980 min (1434 ± 169 s/nest, range 120–3960 s/nest, range of dates 23 June–14 July). In the Unfed treatment, 64 nests were monitored for a total of 639 min (597 ± 69 s/nest, range 75–2952 s/nest, range of dates 29 June–17 July). The difference in total observation time and observation duration per nest between the two treatments is due to the low survival rate of B-chicks of the Unfed group (see Results) leading to a reduction in the number of two-chick broods. For the same reason, more observations were carried when the A-chick was under 5 days old than in later stages (0–5 days: 742 min; 5–10: 487 min; 10–15: 274 min; 15–20: 116 min) with a decreasing proportion of observations in the Unfed treatment.

As aggressive behaviour cannot be recorded when parents are brooding, we opportunistically observed chick behaviour when parents stood up. If several parents stood up simultaneously we randomly chose one focal nest. A stopwatch was started as soon the parent stood up and chick behaviour was recorded until the parent brooded again or for 120 s. During these observations, we recorded aggressive behaviour as well as begging and feeding behaviour of both chicks. A chick was considered to show aggressive behaviour when it pecked at its sibling. The frequency of aggression was calculated by dividing the sum of all aggressive bouts (any attack series with pauses of less than 5 s) by the total duration of the observation. The intensity of aggression was measured using the following scores: 0 for no aggression, 1 for weak aggression (31% of all aggression events), 2 for moderate aggression (48%) and 3 for intense aggression (21%). Begging and feeding rates were calculated by dividing the number of begging events (every time a chick pecked at the parent's bill) or feeding events (every time a chick

swallowed food regurgitated by the parent) by the total observation time.

Data Analyses

Statistical tests were performed with SAS (SAS Institute, Cary, NC, U.S.A.) using general linear mixed models (GLMM; SAS PROC MIXED). As many broods were observed repeatedly, often at different ages and at different times of the same day, we included the nest (nested in treatment) as a random variable in the model to avoid pseudoreplication and included chick age and time of day as covariates as fixed effects (reported when significant). We thus started with a full model with multiple interactions and used a stepwise backward elimination of variables. Only the significant interactions are reported in the Results. When there was only one value of a response variable per nest, for chick growth or survival for instance, we calculated the mean value of the independent variable and took into account the number of observations per nest by using the 'weight' option in the general linear model (GLM) procedure. Chick survival (or life expectancy) was calculated as the mean age of death or ejection from the nest. For chicks that survived until fledging we considered for the purpose of analyses a life expectancy of 45 days, which is the mean age at fledging in this colony. For all analyses, we verified the normality of the distribution of data and the homogeneity of variance across groups. Sample values are expressed as mean \pm SE throughout.

RESULTS

Effects of Treatment

The treatment had a significant effect on laying date (average laying date: Fed: 31 May; Unfed: 5 June) and hatching date, with chicks from the Fed group hatching on average 5.5 days before those of the Unfed group (GLM: $F_{1,103} = 50.50$, $P < 0.0001$ for both laying and hatching date). The treatment did not, however, have any effect on the mean hatching weight of either A-chicks (GLM: $F_{1,101} = 0.01$, $P = 0.93$) or B-chicks (GLM: $F_{1,100} = 0.08$, $P = 0.78$). Furthermore, the treatment had no effect on the hatching asynchrony between A-chicks and B-chicks (GLM: $F_{1,103} = 1.36$, $P = 0.25$).

Fed parents fed A-chicks significantly more than Unfed parents (GLMM: $F_{1,103} = 4.02$, $P = 0.047$; Fig. 1), taking into account the negative effect of chick age ($F_{1,103} = 10.89$, $P = 0.001$). There was, however, no significant difference in the feeding rate of B-chicks

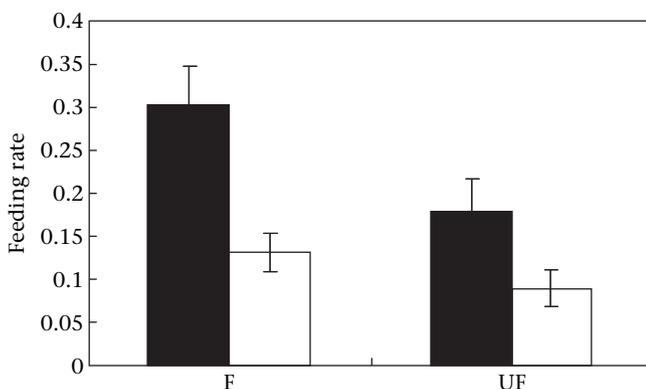


Figure 1. Mean feeding rate (number of food ingestion events/total observation time \times 100) of A-chicks (black bars) and B-chicks (white bars) according to the experimental treatment. F: chicks whose parents received supplemental food, $N = 41$ broods; UF: chicks of control parents (Unfed), $N = 64$ broods. Error bars represent SEs.

(GLMM: $F_{1,103} = 1.35$, $P = 0.25$). The treatment had no effect on the begging frequency of A-chicks (GLMM: $F_{1,103} = 2.40$, $P = 0.12$; with age as a significant covariate: $F_{1,103} = 8.25$, $P = 0.005$).

A-chicks from the Fed treatment group gained significantly more weight between 0 and 15 days of age than those from the Unfed group (GLM: $F_{1,85} = 10.27$, $P = 0.002$; Fig. 2). However, we found no significant difference in A-chick life expectancy (GLMM: $F_{1,103} = 1.17$, $P = 0.28$; 37.92 ± 1.40 days).

Aggressive Behaviour

Aggression frequency and intensity were highly dependent on chick age (GLMM: frequency: $F_{1,103} = 11.20$, $P = 0.001$; intensity: $F_{1,103} = 30.73$, $P < 0.0001$), A-chicks becoming much less aggressive as they got older. Furthermore, we found that A-chicks of the Fed group were significantly less aggressive than those of the Unfed group, in terms of both frequency (GLMM: $F_{1,103} = 4.99$, $P = 0.028$; Fig. 3a) and intensity (GLMM: $F_{1,103} = 6.46$, $P = 0.013$; Fig. 3b).

We found a significant effect of the growth (weight gain between 0 and 10 days) of the A-chick on its aggressiveness during that period in interaction with the treatment (GLM: $F_{1,78} = 10.89$, $P = 0.002$). In other words, in the Unfed group (but not in the Fed group), the faster the A-chick grew the less aggressive it was towards its younger sibling (GLM: $F_{1,43} = 7.04$, $P = 0.011$; Fig. 4). Furthermore, we explored the link between begging and feeding rate of the A-chick and its level of aggression. After taking into account the effect of the treatment (no significant interaction), we found no relationship between chick feeding rate and aggressiveness (GLMM: $F_{1,52} = 2.16$, $P = 0.15$), but did find a positive relation between begging rate and the intensity of aggression (GLMM: $F_{1,52} = 9.71$, $P = 0.002$) in all chicks regardless of treatment.

Relation Between A-chick Aggression and B-chick Traits

When aggression occurred, its frequency affected B-chick begging frequency negatively (GLMM: $F_{1,85} = 4.46$, $P = 0.038$; Fig. 5) but not feeding frequency (GLMM: $F_{1,85} = 0.09$, $P = 0.77$). We found a significant negative correlation between mean intensity of aggression by A-chicks and weight gain of B-chicks between hatching and 5 days of age (GLM: $F_{1,43} = 6.40$, $P = 0.015$; Fig. 6a). B-chick life expectancy was highly correlated with both aggression

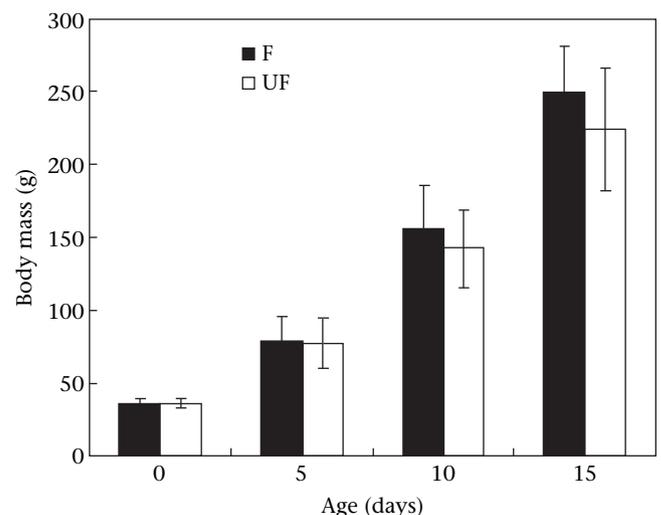


Figure 2. Mean A-chick body mass (g) at 0, 5, 10 and 15 days of age in Fed (F; respective sample size: 41, 40, 37 and 36 chicks) and Unfed (UF; $N = 62, 59, 54$ and 53 chicks) treatments. Error bars represent SDs.

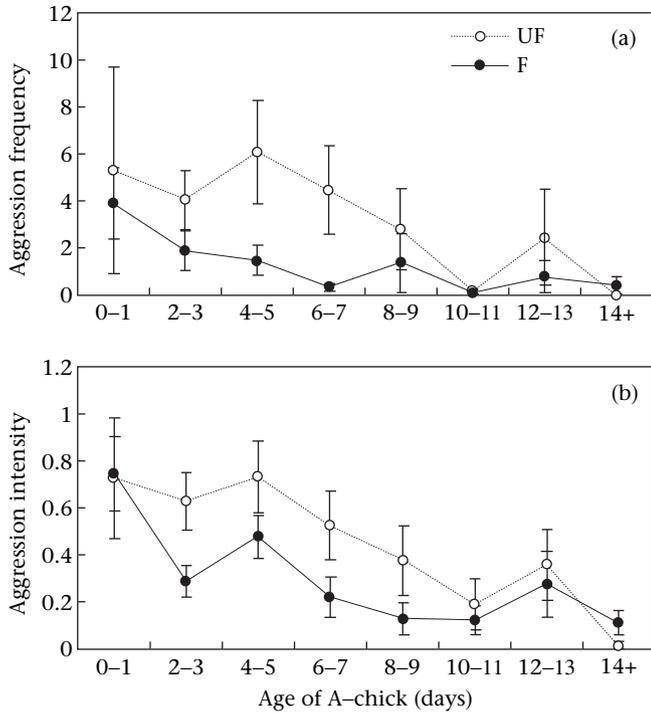


Figure 3. (a) Mean aggression frequency (total aggression duration/total observation time \times 100) and (b) mean aggression intensity (a score ranging from 0 to 3; see Methods) of the A-chick according to A-chick age (days) in the Fed (F; $N = 318$ observations for each variable) and Unfed (UF; $N = 200$ observations for each variable) treatments. Error bars represent SEs.

frequency (GLM: $F_{1,96} = 8.02$, $P = 0.006$) and aggression intensity (GLM: $F_{1,96} = 8.43$, $P = 0.005$; Fig. 6b) of the A-chick. B-chick life expectancy was highly dependent on treatment (Fed: 26.20 ± 3.12 days; Unfed: 13.59 ± 1.89 days; $F_{1,96} = 18.25$, $P < 0.0001$) but that variable did not interact with aggression intensity or frequency.

DISCUSSION

Effects of the Treatment

Our food supplementation experiment showed that several breeding parameters are affected by food availability. First, eggs were laid 5–6 days earlier in Fed pairs than Unfed pairs. Second, considering only A-chicks, as traits of the B-chick depend largely on

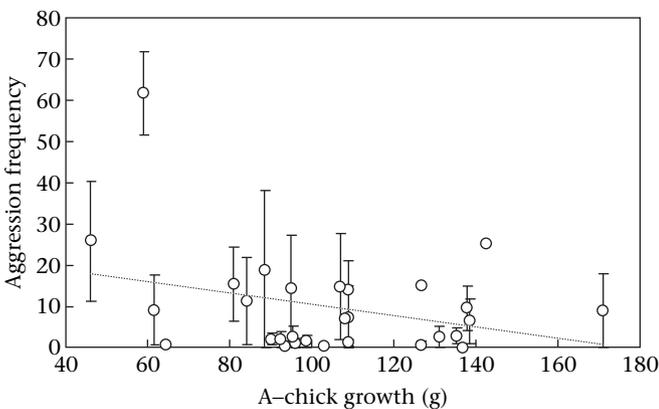


Figure 4. Mean aggression frequency between 0 and 10 days in relation to weight gain (g) for A-chicks between 0 and 10 days of age (Unfed group). $N = 34$ broods. Error bars represent SEs.

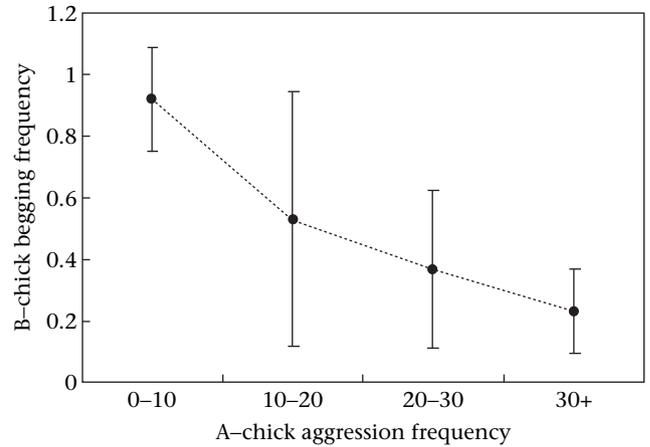


Figure 5. Mean B-chick begging frequency (beggings/total observation time \times 100) at four levels of aggression frequency by the A-chick. Fed and Unfed groups are combined as there was no significant effect of the treatment. $N = 157$ observations. Error bars represent SEs.

the behaviour of its older sibling, we showed that chicks whose parents were food supplemented were fed more frequently than chicks of control parents. Third, this treatment resulted in chicks of the Fed group having a higher growth rate than 'Unfed' chicks. These results confirm previous evidence that, in our study population, several breeding parameters are sensitive to food supplementation (Gill et al. 2002), as anticipated by the overall poor productivity of kittiwakes in the Pacific region (Gill & Hatch 2002).

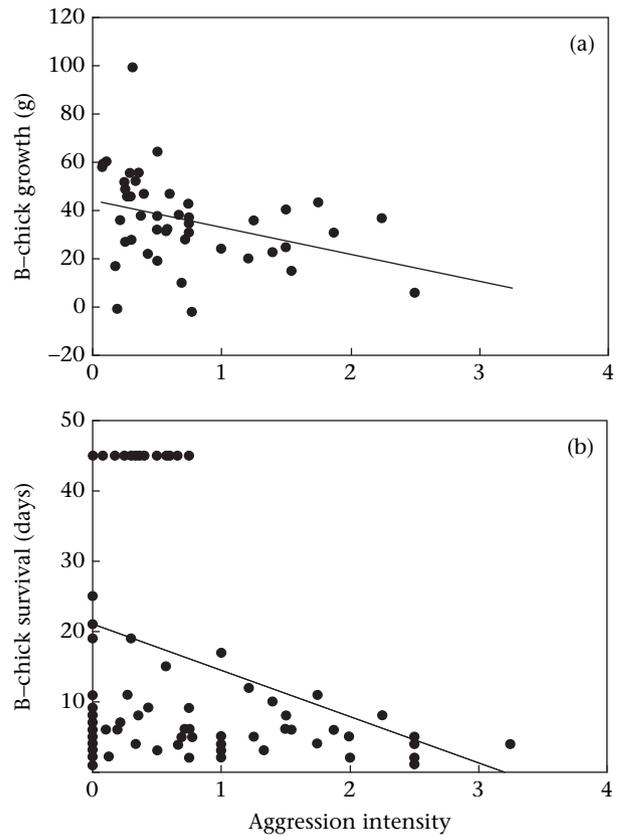


Figure 6. (a) Weight gain of B-chicks between 0 and 5 days of age ($N = 45$ broods) and (b) mean B-chick survival ($N = 98$ broods) according to mean A-chick aggression intensity. Fed and Unfed groups are combined as there was no interaction between treatment and aggression intensity.

The experimental treatment seemingly had no effect on A-chick survival or begging, again confirming what was found by Gill et al. (2002). This lack of effect on A-chick survival can be explained by the fact that the older sibling has first access to food and therefore obtains sufficient food to survive even when overall food availability is low. B-chick survival is much more sensitive to food supply, the younger sibling acting as a 'fuse' when environmental conditions are poor (Forbes et al. 2001). The lack of a difference in A-chick begging rate is more difficult to explain. It could be that chicks have evolved to beg at a high frequency whatever their level of satiation to secure maximum food provisioning.

Effects of Food Supplies on Chick Aggressiveness

One of the main results of this study is that a sustained increase in food availability led to a highly significant decrease in both frequency and intensity of aggressiveness of the A-chick towards its younger sibling. Our experimental set-up associated with the particular context of food shortage experienced by our study population provided several advantages. First, it allowed us to manipulate the amount of food ingested by chicks indirectly, via the parents. We thus avoided intrusive manipulation of chicks and were able to rule out effects of the manipulation itself and of frustration on chick behaviour. Second, ingestion was manipulated not by food deprivation but rather by increasing food levels in the Fed group. This shows that aggression levels are affected by both downward (e.g. Drummond & Chavelas 1989; Irons 1992; Machmer & Ydenberg 1998; Cook et al. 2000) and upward manipulation of food amount thus confirming its role as a proximate factor. Our results corroborate those of Hodge et al. (2009), who used a similar upward manipulation in food supplies, although in a nonsiblicidal species. Third, the manipulation was sustained throughout the reproductive season and more particularly the nestling period, which enabled us to investigate the consequences of a long-term increase in food supplies.

Our experimental design did have certain drawbacks though. The lack of a real control (e.g. sham feeding) prevented us from excluding the possibility that the supplemental feeding disturbed the chicks or caused a change in parental behaviour inducing a reduction in aggression. Chick disturbance, however, seems unlikely as chick behaviour was recorded outside of feeding periods. Regarding the change in parental behaviour, supplemental feeding has been shown to affect male and female attendance at the nest for instance (Gill et al. 2002). Such a change could affect levels of chick aggression, although this remains to be proven. In addition, the supplementary feeding of parents during prelaying and incubation periods does not allow us to discount alternative proximate causes of broodmate aggression totally. Increased food supplies during oogenesis may have induced maternal effects, such as changes in hormone levels deposited in the egg yolk (Schwabl 1997), which can affect chick behaviour (Muller et al. 2009). This hypothesis and the FAH are not mutually exclusive and may actually have additive effects. None the less, the latter seems more parsimonious and is more supported by evidence, in facultatively siblicidal species at least (reviewed in Drummond 2001b). Despite these minor drawbacks, our results add new lines of evidence which complement that of previous studies (Drummond & Chavelas 1989; Machmer & Ydenberg 1998; Cook et al. 2000) and altogether provide new support for the FAH (Mock 1987; Drummond 2001b).

Effects of Age, Growth and Begging on Aggressiveness

We found that, regardless of the experimental treatment, both frequency and intensity of aggression were highly correlated with chick age, with a 10-fold decrease in levels of aggression between 1 and 12 days of age. This pattern has been reported in a number of

other species (Mock & Lamey 1991; Pinson & Drummond 1993; Drummond 2006) and supports the early dominance establishment hypothesis (Mock 1985; see also Valderrabano-Ibarra et al. 2007). According to this hypothesis, elder chicks attack their sibling early in the nestling period to establish a dominance relationship that ensures their feeding priority later on, when their food requirements will be much greater. The advantage of being aggressive at very early stages is that B-chicks have only just hatched and are least capable of defending themselves because of the proportionately large age difference at that time.

Monitoring aggressive behaviour of A-chicks for up to 20 days after hatching enabled us to examine the factors controlling broodmate aggression. We found a negative correlation between A-chick growth rate and aggression frequency (only in the Unfed group, levels of aggression probably being too low in the Fed group). In other words, poorly fed chicks showed a higher propensity to attack their younger sibling. Furthermore, higher levels of begging by the elder chick were associated with higher intensities of aggression. Both outcomes suggest that it is the amount of food received, and more precisely the level of satiation, that triggers A-chick aggressiveness. This is consistent with previous work focusing on the proximate causes of broodmate aggression (reviewed in Drummond 2001a, b).

Effects of Aggression on B-chick Traits

The first consequence of A-chick aggression on B-chick behaviour was that the more the A-chick attacked its sibling the less the latter begged for food, confirming what has been found in a number of other facultatively siblicidal species (reviewed in Drummond 2002). There are two main ways in which A-chick aggressive behaviour may prevent the B-chick from begging. It may be that by frequently attacking the younger sibling the older chick effectively exhausts the time and energy that its younger sibling would have otherwise devoted to begging. Alternatively, repeated attacks may intimidate and subdue the younger chick, dissuading it from begging. As aggressive behaviour decreased begging rate significantly, we expected this aggression to affect B-chick feeding rate as well. However, no significant relationship was found. Since begging behaviour is typically devoted to securing food from parents, this is a surprising result. Although we monitored a substantial number of nests over several days, observations of feeding by B-chicks were rare. Thus it may be that we lacked the statistical power to detect such a correlation. Alternatively, it is possible that feeding decreased in ways we were unable to detect (e.g. smaller food amounts per feeding event or less feeding at night for instance). Nevertheless, the fact that the average aggression intensity was negatively correlated with B-chick growth rate suggests that A-chick agonistic behaviour did negatively affect the B-chick's access to food. The last main finding is that B-chick survival was highly correlated with A-chick aggressiveness. We found that a slight change in the level of aggression had a large effect on B-chick survival, with moderate aggression reducing life expectancy from 22.5 to 6.5 days. Aggression could therefore be a beneficial strategy for the A-chick as it rids the elder sibling of competition for resources early on, before the B-chick's food requirements become substantial and before the B-chick is capable of defending itself. Considering the relationship between aggressive behaviour and several B-chick traits, we found a cumulative process by which aggression of the A-chick leads to brood reduction.

Supplemental Feeding of Parents as a Proxy of Environmental Food Availability?

As stated above, supplemental feeding of breeding pairs led to an earlier laying date, an increase in chick feeding rate and an

increase in growth rate. These three parameters have been shown to vary in response to environmental conditions in several studies of kittiwakes and other seabirds (laying date: Coulson 1968; Perrins 1970; Monaghan et al. 1989; feeding rate: Wanless & Harris 1992; Roberts & Hatch 1993; chick growth rate: Monaghan et al. 1989; Barrett & Rikardsen 1992; Hamer et al. 1993). The congruence between these observations and the effects of our experimental treatment, associated with the fact that food supplementation has been shown to increase overall productivity (Gill & Hatch 2002) as well as several other breeding parameters (Gill et al. 2002), suggests that, in our particular study population, supplemental feeding may emulate variations in environmental food availability. If that is the case, our results would provide experimental support for the notion that siblicidal aggression is adaptive, as they relate food supply levels to broodmate aggression levels (as have Hodge et al. 2009 in a different context) and corroborate observations of kittiwakes by Braun & Hunt (1983) and Irons (1992), who noted higher levels of chick aggression and siblicide in years of food shortages. Thus increased aggression under conditions of food shortage would provide a mechanism by which brood sizes are adjusted to food resources during the nestling period.

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