Is broodmate aggression really associated with direct feeding?

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Summary

The Feeding Method hypothesis (FMH) proposes that the way parents transfer food to chicks influences whether broodmates compete for it aggressively or non-aggressively. The FMH assumes that aggression is more efficient for securing a large share of food when prey items pass from bill to bill (direct feeds) than when prey is deposited on the nest floor (indirect feeds). In species with a developmental transition from indirect to direct feeding, the hypothesis predicts more aggression during direct than indirect feeds and an increase in rates of aggression as feeding becomes increasingly direct. We quantified development of aggression and feeding in two-chick cattle egret (*Bubulcus ibis*) broods in order to test the FMH's assumption and its two developmental predictions. We also examined whether changes in rates of aggression early in the nestling period are better predicted by the Feeding Method, Food Amount or Early Dominance Establishment hypotheses. Neither the assumption nor either of the predictions of the FMH was supported and, if anything, senior broodmates were more aggressive early in the nestling period when feeding was indirect. These observations cast doubt on the ultimate influence of feeding method on use of aggression and, especially, on the role of direct feeding as a proximate trigger for aggression. Rates of aggression better fitted the temporal patterns predicted by Early Dominance Establishment and Food Amount hypotheses.

Keywords: broodmate aggression, feeding method, food amount, dominance, submission, cattle egret.

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Introduction

In parentally fed avian species, broodmates generally compete for limited parental food by begging and scrambling (Rydén & Bengtsson, 1980; Royle et al., 2002), but in a diverse minority of species competition also involves pecking and biting (Mock & Parker, 1997; Drummond, 2002). In these aggressive species hatching asynchrony confers a competitive advantage to elder chicks and a dominance hierarchy is established early in the nestling period (Drummond et al., 1986; Mock & Parker, 1997). Senior chicks (first-hatched in a brood) intimidate younger siblings and exclude them from parental feeds, thereby obtaining more than their share of food (Mock, 1985; Ploger & Mock, 1986; Drummond, 2002). Aggression can lead to death of younger siblings through forced starvation, expulsion from the nest or lesions (Mock, 1985; Mock & Parker, 1997; Drummond, 2001a).

Parents transfer food to chicks either indirectly, by depositing whole, predigested or dismembered prey items on the nest floor, from where chicks peck or tear pieces they can swallow, or directly, from parental bill to chick's bill. According to the Feeding Method hypothesis (FMH; Mock, 1984, 1985), selection favours the use of aggression by species with direct feeding, provided chicks have the ability to constitute a potential threat to one another and parentally provided food is limiting. Although the hypothesis appeared to propose that the size of the prey transferred to the chick influences aggression (presented as Prey Size hypothesis: Mock, 1985), it is the method of transfer (feeding method) that is the key factor. Hence, the hypothesis is purportedly supported by sibling aggression in some large predatory species, such as boobies, pelicans and raptors, in which parents predigest or dismember large prey and deliver them in small parcels into chicks' beaks (Mock, 1985). For this reason, the Prey Size hypothesis was reassessed and labeled the FMH (Drummond, 2001b). According to the FMH, at the ultimate level feeding method has determined the distribution of siblicidal aggression among species and at the proximate level feeding method acts as a trigger for use of aggression (Mock, 1984).

The FMH hinges on the untested assumption that aggression is more efficient for securing a large share of food during direct feeds than during indirect feeds (e.g., Mock & Parker, 1997, p. 106). Supposedly, when food comes directly from the parent, intimidation of competitors yields exclusive access to the parental bill and bolus; when food is on the floor, it is equally available to all and success depends on handling speed (Mock & Parker, 1997, p. 103). Several species, including some ardeids and pelicanids, show a developmental change in feeding method. Young chicks are initially fed indirectly; then, as they grow and mature they switch progressively to catching boluses directly from the parental bill (Mock, 1985; Ploger & Mock, 1986; Pinsón & Drummond, 1993). From this follows the prediction of a proximate effect of feeding method: chicks will facultatively adopt either aggressive or non-aggressive competition according to whether food is provided directly or indirectly. "The logic of the hypothesis also requires that any changes in fighting be accompanied by a switch to the appropriate feeding techniques (and degree of food control). Embedded in this approach is the tacit assumption that the birds possess sufficient developmental flexibility to make such adjustments, that is, to modify their behavioral ontogeny radically as a function of the cue" (Mock & Parker, 1997, p. 116).

Support for the FMH comes from two descriptive studies and an experiment comparing aggression of indirectly fed and directly fed broods in two ardeid species (Mock, 1984, 1985; Mock et al., 1987a). However, the studies have been criticized, among other reasons because they failed to control adequately for food deprivation and because some of their results actually contradict the FMH (Drummond, 2001a). To date no study has tested the hypothesis' assumption that aggression is more profitable during direct feeds than during indirect feeds. Furthermore, although the ardeid studies supporting the hypothesis documented temporal changes in feeding method, they did not analyse temporal variation in rates of aggression nor relate changes in aggression to changes in feeding method.

The scarce developmental data available do not appear to support the prediction of a proximate effect of feeding method on use of aggression. Great egret and great blue heron chicks fought vigorously during their first month of life despite being indirectly fed (Drummond, 2001b), and there was no evidence for increased aggression by brown pelican (*Pelecanus occidentalis*) chicks as their feeding switched from indirect to direct (Pinson & Drummond, 1993).

The assumption that aggression is more profitable during direct feeds than during indirect feeds and the developmental prediction that rates of aggression should increase as feeding becomes increasingly direct can both be tested by quantifying feeding and aggression during the developmental change in feeding method. However, any such analysis must also take into account additional potential influences on rates of aggression, such as food amount and establishment of dominance which could provide alternative explanations for changes in the patterns of aggression. The Food Amount hypothesis (Mock et al., 1987a; Drummond, 2001a) predicts that a dominant nestling's aggression will increase as its food ingestion declines. In the majority of bird species, daily food requirements of chicks increase with age to a maximum about midway through growth and then either decline or plateau (Weathers, 1996). When a brood's food requirements are at their maximum and parents probably have most difficulty satisfying them, nestling aggression is likely to be exacerbated by underfeeding (somewhat paradoxically, because ingestion is at its developmental peak). It is unresolved whether food amount has a proximate influence on aggression in ardeid species as it does in some other avian species (Drummond, 2001a; cf., Mock et al., 1987a,b), and only one ardeid study clearly shows that poorly fed individuals are more aggressive (Creighton & Schnell, 1996).

According to the Early Dominance Establishment hypothesis, elder chicks attack their broodmates early in the nestling period to establish the dominance relationships that will ensure their feeding priority later on (Mock, 1985; Pinson & Drummond, 1993; Drummond, 2006). Mock & Lamey (1991) suggested that aggression in ardeid broods declines during the first 3 weeks due to the establishment of dominance relationships. The hypothesis predicts that aggression should first increase sharply as senior hatchlings develop their aggressive potential, then peak and decline to a low level after dominance-subordination is established. It also predicts that rebelliousness of junior chicks (i.e., aggressive resistance of the senior chick's bid for control) should show an early increase, peak and decline. Rebelliousness of junior ardeid chicks could be expressed by: (1) more total pecks per fight (summing pecks of both chicks) if juniors peck back when attacked or require more pecks to respond with submission, (2) junior chicks initiating a greater proportion of fights or (3) a higher proportion of pendulum fights (two chicks facing each other, at close range, pecking in turns; Milstein et al., 1970).

Cattle egret (*Bubulcus ibis*) chicks compete aggressively for parentally provided food and switch progressively from indirect to direct feeding as they develop (Ploger & Mock, 1986). Both parents care for chicks, which fledge on average at 32 days of age (Martínez-Vilalta & Motis, 1992). Broods in Texas were fed an average 5.2 boluses in each of 3.0 meals per day (Ploger & Mock, 1986). Violent aggression between broodmates involves mainly pecks, but also bites. Mortality of last hatched chicks is common. In three-chick broods, 67% of last-hatched chicks died in 15 broods in Texas (Ploger & Mock, 1986), 33% in 100 broods in Oklahoma (Mock & Parker, 1997) and 85% in a South African population (Siegfried, 1972). In 161 two-chick broods of a South African population, 15.8% of chicks died before fledging and 61% of deaths were attributed to starvation (Siegfried, 1972).

We report the first quantification of developmental variation in rates of aggression in an ardeid. Our study examines the ultimate influence of feeding method on aggressive competition by testing whether aggression secures for chicks a larger proportion of food during direct than indirect feeds. It also examines the proximate influence of feeding method on aggressive competition by testing whether aggression is greater during direct than indirect feeding and whether it increases as feeding becomes increasingly direct. Finally, it examines whether temporal changes in rates of aggression are better predicted by the Feeding Method, Food Amount or Early Dominance Establishment hypotheses.

Methods

From mid-June until the end of July 2003, four observers studied cattle egret broods in a dense, mixed species colony, on a 12 by 15 m mangrove (*Rhizophora mangle*) islet in a coastal brackish lagoon at La Mancha, Veracruz, Mexico (19°24′ N and 96°24′ W).

Twenty nine accessible nests were selected and individually marked with numbered plastic tags, mostly between clutch completion and hatching but in two cases after the eggs had hatched. Average clutch size before hatching was 2.71 eggs (range = 1-5) and 2.00 chicks hatched per nest on average (range = 1-3 d, $N = 28$ nests). In the nests marked before hatching, first and second chicks hatched 2.29 days apart (range = 1-7 d, $N = 14$ clutches), while second and third chicks hatched 2.00 days apart (range = 1-3 d, $N = 6$ clutches). We observed behaviour in nine young and visually accessible two-chick broods of the sample, after marking chicks on the crown and rump with non-toxic acrylic paint: red for first hatched (senior) and black for second hatched (junior) chicks. Color marks have no apparent effect on dominance hierarchies or other behaviour of chicks (Ploger & Mock, 1986).

Observations were made from three floating wooden towers (observation nests were at or below observer eye-level) stationed 16-17 m from the edge of the colony. Egrets were habituated to the daily activities of the fishermen in the lagoon and observers did not appear to affect their behaviour. All nine broods were observed during two 3-h periods (0730-1030 h and 1600-1900 h) on a daily basis from completion of hatching (mean: 5.6 d of age of the senior chick, range = 4-11 d) until the senior chick was 20 d old, except when it rained. Each observer watched a maximum of three broods simultaneously. Preliminary observations showed that egret activity levels varied little between midday, morning and afternoon periods; thus, the two 3-h observation periods allowed representative sampling of daily activity.

Observers recorded all feeding bouts and fights, largely following the sampling methods of Mock (1985) and Ploger & Mock (1986). Those studies focused on larger broods, but the relevant hypotheses and methods are not brood-size specific. For each food delivery observers noted the size of the bolus (classified from 1 to 4) by comparing it with the length of the adult's beak, the visually estimated proportion (in tenths) of the bolus ingested by each chick and the feeding method of each chick (indirect or direct). We multiplied the proportion of each bolus ingested by a particular chick by the bolus size and summed across all boluses delivered during the bout to obtain the 'food amount units' (FAU) ingested by each chick during each bout. A bout began when the adult regurgitated the first bolus and ended when no more boluses were regurgitated during 10 min. We regarded a feeding bout as indirect if at least 70% of boluses touched the nest floor before being ingested by one of the chicks or direct if at least 70% of boluses were taken from the adult's beak. These criteria are broader than the criteria based on a value of 80% used by Mock (1985) for a different purpose: dividing the nestling period into phases. Using criteria based on 70% rather than 80% enabled us to increase sample sizes for analyzing the assumption of the FMH; it had no influence on the direction of differences found and had little influence on their magnitude.

We registered a peck when a chick forcefully made contact with its beak on any part of a broodmate's body and a bite when a chick pressed any part of a broodmate's body between its mandibles. Summed pecks and bites are referred to as attacks. A fight began with the first attack and ended when attacking did not occur for at least 10 s. For each fight, observers noted which chick attacked first and the number of attacks delivered by each chick. Observers also noted whether each fight took place during a feeding bout, that is, if it took place within 1 min before the first bolus was delivered or within 10 min after the last bolus was delivered.

The three measures of junior chick rebelliousness were calculated for each brood on each day: (1) proportion of fights initiated by the junior chick is the number of fights where the junior attacked first divided by total fights, (2) proportion of pendulum fights is the number of pendulum fights divided by total fights and (3) fight length is the number of attacks per fight.

We tested the assumption that aggression is more efficient for securing large shares of food during direct feeds than during indirect feeds using only senior chicks (the main aggressors). Feeding bouts were classified as 'with attacks' when seniors pecked or bit their broodmate at least once during the bout. We calculated the average proportion of FAUs ingested by each senior chick for all of its indirect feeds with and without aggression as well as for all of its direct feeds with and without aggression for each day. However, not all broods presented feeding bouts of all four categories, thus sample sizes (numbers of broods) in our comparisons varied.

All statistical comparisons involved the mean of several behavioural scores for either the junior or the senior chicks of each of several broods, and sample sizes given are the numbers of broods included in each analysis. We present means and standard errors except when non-parametric analyses were used, when we present medians. Averages presented in Results are calculated across broods. For example, the average age when senior chick rate of aggression peaked was based on the average of the nine ages at which each of the nine senior chicks reached its individual peak. On the other hand, graphs show, for each chick age on the x-axis, the average of the behavioural scores (e.g., number of attacks) of all seniors or juniors observed at that age, with the exception of Figure 2. Note that the age at which a behavioural peak or inflection occurred for the total sample shown in the figures is not necessarily the same as the mean of the peaks and inflections of the N individuals in the sample.

For parametric analyses yielding non-significant results, we present 95% confidence intervals (95% CI) for the difference between means rather than the power of the test, as suggested by Hoenig & Heisey (2001) and Colegrave & Ruxton (2003). If a comparison between two samples is non-significant, the 95% CI includes zero. As the samples become increasingly different the CI becomes wider and more asymmetric around zero.

Results

There was no mortality in any of the 9 observation broods, at least until 20 d of age of the senior chick. In 30% of the marked broods at least one chick died: one of 7 single-chick broods, 3 of 17 two-chick broods and all 5 three-chick broods were reduced.

In all 9 observation broods, chicks competed aggressively and both seniors and juniors attacked and initiated fights. We observed 0.48 ± 0.07 fights/h during the nestling periods of the 9 broods (ages 4-20 d), and junior chicks initiated 11.9 ± 2.3% (range = 2.7-25.6%, $N = 9$) of the fights in their broods. Pendulum fighting occurred in 16.1 ± 3.7% (range = 2.3-31.8%, $N = 9$) of observed fights, mostly between 8.3 and 12.6 d of senior chick age. Juniors, and on some rare occasions seniors, conceded fights by fleeing or, more often, by crouching in the bottom of the nest, after which attacks stopped. Both senior and junior chicks participated in all feeding bouts, and did so by begging and scissoring the parental bill.

Chicks in all nine broods fed indirectly at first then switched progressively to direct feeding. The transition took about four days, with senior and junior chicks, respectively, starting to switch at ages 7.7 ± 0.42 d and 7.3 ± 0.41 d and feeding predominantly directly (>70% of boluses taken directly) by ages 12.1 ± 0.73 d and 11.4 ± 1.1 d ($N = 9$; see Figure 1). From age 5.6 d (range 4-11 d) until age 20.0 d, the nine senior chicks ingested 13.8% more food than their junior broodmates (median senior = 1.24 FAU/h, junior = 0.94 FAU/h; Wilcoxon matched pairs: $Z = 2.67$, $N = 9$, $p = 0.008$). When we compared seniors and juniors at the same age (from 4 to 18 d of age), thus controlling for the potentially confounding effect of age differences due to asynchronous hatching, senior chicks ingested 17.3% more food than junior broodmates (average senior = 1.49 FAU/h, junior = 1.05 FAU/h; Paired *t*-test: $t8 = 3.47$, $p = 0.008$).

Seniors attacked their junior broodmates 5.8 times more often than vice versa (median attacks by senior = 0.9 attacks/h, attacks by junior = 0.2 attacks/h; Sign test: $p = 0.039$, $N = 9$). In a single brood this trend was reversed, with the junior chick attacking 1.2 times more often than its senior broodmate, while the senior ingested only 2.7% more food despite being one day older than the junior chick. Average rates of aggression were higher in our population than those reported in previous studies: 0.1 attacks/h by the A-B dyad (eldest and second hatched chicks) and 0.2 attacks/h by the B-C dyad (second and third hatched) in a Texas population observed until the senior was 25 d old (Ploger & Mock, 1986) and 0.02 fights per day in two-chick broods of a Japanese population observed until the senior was about 60 d old (well beyond fledging; Fujioka, 1985).

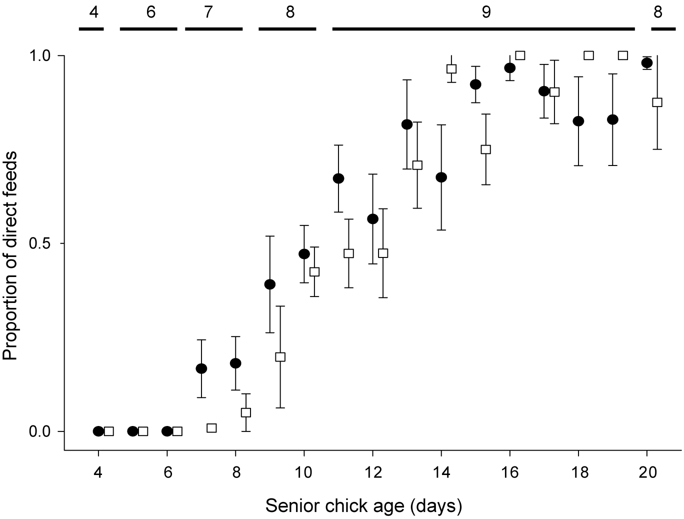

Figure 1. Developmental transition from indirect to direct feeding. Proportion of feeds ($\bar{X} \pm$ SE) which were direct for both senior (●) and junior (☐) chicks as a function of senior chick age. Numbers along the top indicate number of broods.

Feeding Method hypothesis

Contrary to the critical assumption of the FMH, seniors did not ingest a larger proportion of food during direct feeding bouts with attacks (mean = 58%) than during direct bouts without attacks (mean = 60%; t-test: $t8 = -0.21$, $p = 0.84$, 95% CI of difference between means: −0.28-0.23; Figure 2). This result was unchanged when we restricted the sample to the period when intimidation of the junior chick presumably was largely established, after age 7 d of the senior chick (respective means 62% and 55%; Mann-Whitney $U = 18.5$, $p = 0.61$, $N = 14$). More importantly, seniors did not ingest a larger proportion of food during direct bouts with attacks (mean = 58%) than during indirect bouts with attacks (mean = 56%; t-test: $t6 = -0.83$, $p = 0.44$, 95% CI of difference between means: −0.30-0.15; Figure 2). Finally, senior chicks did not ingest a larger proportion of parentally provided food during indirect feeding bouts with attacks (mean = 56%) than during indirect bouts without attacks (mean = 61%; t-test: $t8 = 1.02$, $p = 0.34$, 95% CI of difference between means: −0.75-0.19; Figure 2). Although sample sizes were small for these comparisons, mean values were surprisingly similar for all categories, variance was relatively low and the 95% CI of difference between means were narrow and relatively

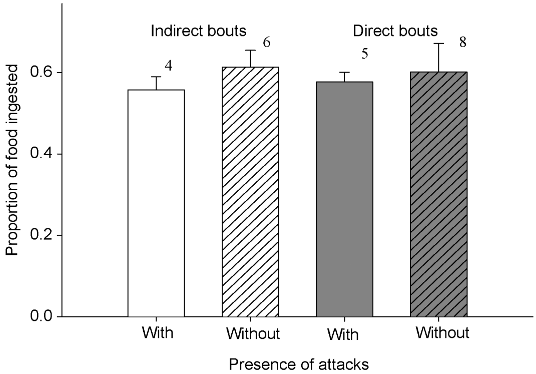

Figure 2. Profitability of senior chick's aggression during indirect and direct bouts. Proportion of food ingested by the senior chick ($\bar{X} \pm$ SE) during indirect and direct bouts, with and without attacks. Numbers above the bars are the number of broods.

symmetric around zero. We could not test whether the increase in proportion of food ingested achieved using aggression during indirect feeds was smaller than the increase in proportion achieved through aggression during direct feeds because we had insufficient broods where we had observations of both indirect and direct feeds with and without aggression. In any case, the means shown in Figure 2 hold out little prospect of there being such a difference.

Contrary to the main prediction of the FMH, senior chicks were just as aggressive during (predominantly) indirect feeding bouts (median = 0.08 pecks/bout) as during (predominantly) direct feeding bouts (median = 0.00; Mann-Whitney U-test: $U = 34.5$, $N = 8$, $p = 0.89$). Furthermore, temporal changes in rates of aggression did not parallel changes in feeding method: aggression increased and peaked before feeding became predominantly direct and by the time feeding was predominantly direct, rates of aggression were close to zero (Figure 3). Finally, when we compared overall senior chick rates of aggression (during and outside feeding bouts) early in the nestling period, when bouts were predominantly indirect (5-8 d of senior chick age), with overall senior chick rates of aggression late in the nestling period, when bouts were predominantly direct (16-19 d of senior chick age), seniors were 28 times more aggressive during the indirect feeding period (1.12 ± 0.49 attacks/h) than during the direct feeding period (0.04 ± 0.03 attacks/h), although the difference fell short of significance (Paired t-test: $t6 = 2.16$, $p = 0.074$, 95% CI of difference between means: −0.43-6.88).

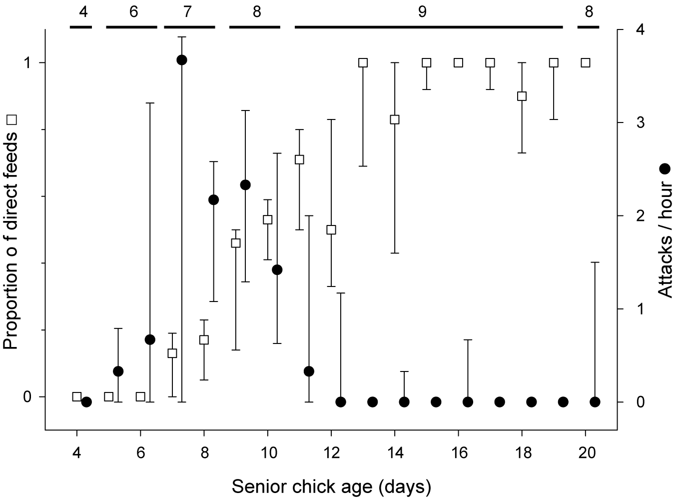

Figure 3. Temporal variation in feeding method and rate of aggression of senior chicks. Symbols represent the median and whiskers the 2nd and 3rd quartiles. Numbers along the top indicate number of broods.

Other hypotheses

As predicted by the Food Amount hypothesis, the peak in the senior chick's rate of aggression, at 10.6 ± 1.3 d of senior chick age, coincided with the peak in food ingested by the brood, at 9.9 ± 0.7 d, and aggression declined roughly when ingestion declined (see Figure 4). The difference between peak ingestion and peak aggression in each brood did not differ significantly from 0. (One sample t-test, $t7 = 1.58$, $p = 0.879$, 95% CI of difference between means: -1.74-1.99; one brood excluded because observations initiated at 11 d of senior chick age.)

As predicted by the Early Dominance Establishment hypothesis, senior and junior chick rates of aggression peaked early in the nestling period, then declined and remained low (Figure 5). The nine senior chicks began attacking their broodmates at age 6.3 ± 0.7 d and their aggression rate peaked at age 10.6 ± 1.3 d, after which it declined and remained at a consistently low level (0.96 ± 0.22 attacks/h from 12 to 20 d of age, $N = 9$). After dominance was established attacks were mostly unidirectional, juniors rarely being aggressive (pers. obs.). Junior chicks also began attacking at an early age (6.0 ± 0.5 d; $N = 9$), even initiating fights as early as 4 d old in 3 cases, and their rate of aggression peaked at 7.0 ± 0.5 d ($N = 9$). Our three

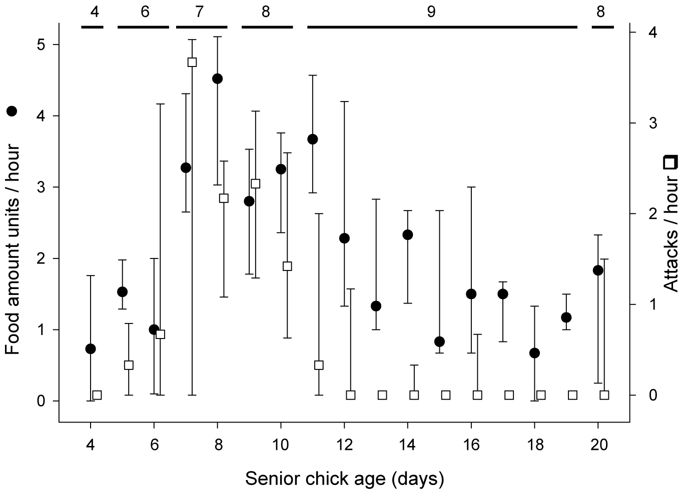

Figure 4. Temporal variation in amount of food ingested by the brood and rate of aggression of senior chicks. Symbols represent medians and whiskers the 2nd and 3rd quartiles, numbers along the top indicate number of broods.

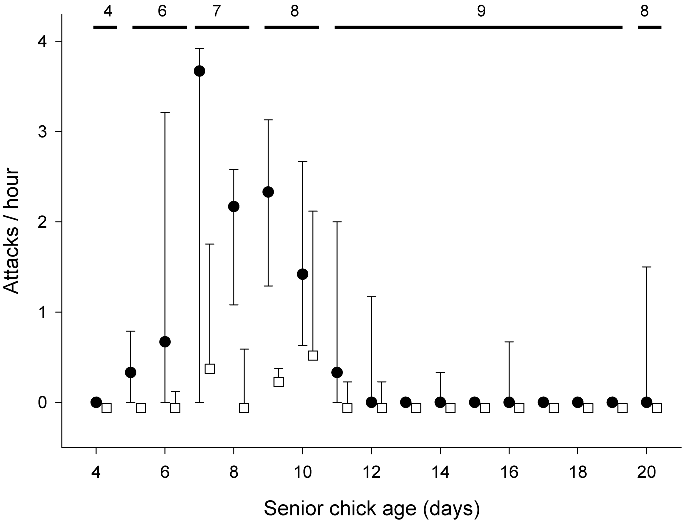

Figure 5. Rate of aggression for senior (●) and junior (☐) chicks as a function of senior chick age. Symbols represent medians and whiskers the 2nd and 3rd quartiles, numbers along the top indicate number of broods.

measures of junior chick rebelliousness showed similar temporal patterns: fight length, proportion of pendulum fights and proportion of fights initiated

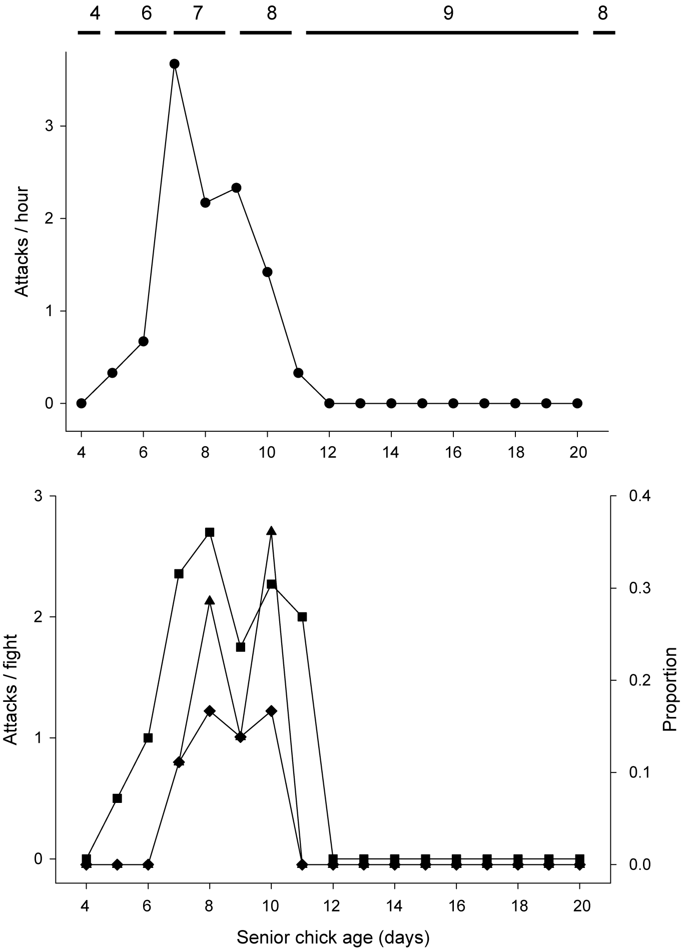

Figure 6. Temporal pattern of aggression by senior chicks and three measures of rebelliousness by junior chicks. Top: senior chick aggression (median) as a function of senior chick age. Bottom: median numbers of attacks by both chicks per fight (■), proportions of pendulum fights (▲) and proportions of fights initiated by the junior chick (◆). Numbers along the top indicate the number of broods.

by the junior chick all showed an early increase and peak followed by a decline as chicks got older (Figure 6). The nine brood average peaks for fight length, proportion of pendulum fights and proportion of fights initiated by the junior chick occurred at similar ages of the senior chick (10.5 ± 1.13 d, 10.44 ± 0.73 d and 9.56 ± 1.13 d, respectively, $N = 9$). Note that the average age at which our three measures of junior rebelliousness peaked coincides closely with the average age at which senior chick aggression peaked (10.6 ± 1.3 d, $N = 9$), and that senior chick aggression decreased to consistently low levels at the same time as junior chick rebelliousness subsided (see Figure 6).

Eight of the nine broods showed similar temporal patterns of change in rate of senior chick aggression, with peaks occurring at similar ages of the senior chick. In the only brood that differed, the pattern of temporal variation in rates of aggression was similar but the increase, peak and decline occurred between the ages 12-16 d of the senior chick. The apparently bimodal pattern of junior chick rebelliousness in Figure 6 results not from individual broods showing a bi-modal pattern but from individual broods peaking at different ages (7-11 d of the senior chick).

Discussion

Senior chicks enjoyed a clear feeding advantage, ingesting 13.8% more food than junior broodmates throughout the nestling period (4-20 d of senior chick age). Even when we controlled for age differences due to hatching asynchrony the difference remained significant. Aggressive superiority throughout the nestling period was demonstrated by senior chicks attacking broodmates nearly six times more than vice versa.

Feeding Method hypothesis

The assumption that aggression should be more efficient for increasing the aggressor's share of food during direct feeds than during indirect feeds was not supported. First, senior chicks using aggression did not obtain a greater proportion of food during direct than indirect feeds, even though most direct feeds occurred after the dominance–subordination relationship was established and most indirect feeds occurred before it was established. However, we cannot rule out that the relative inefficiency of scrambling competition might have been obscured by the large competitive asymmetries between chicks at the early ages when such competition occurred. By the time dominance was established, the large disparity in size and maturity of the broodmates may have largely disappeared and continuation of senior chick's feeding advantage may have depended on their use of aggression. Second, use of aggression during direct feeding did not secure a greater proportion of food, even when the sample was restricted to ages when intimidation of junior chicks was largely established (after the senior chick's peak in aggression). We can be confident that aggression during feeding bouts had little positive effect on how much food the aggressor obtained because the small non-significant differences between our sample values were in the direction opposite to that assumed by the hypothesis, and because the confidence intervals for difference between means were narrow and symmetrical around zero. However, priority of senior chicks during feeding bouts when no aggression was used may have depended on the intimidation effect of their earlier aggression. Third, the benefits of using aggression could be obscured if senior chicks selectively use aggression during bouts when their expected share of food is low while simply scrambling for food when their expected share is high. In sum, our observations cast doubt on the assumption that aggression is more efficient for achieving feeding priority during direct feeds than during indirect feeds but are insufficient to dismiss it.

Our results also failed to support the FMH's developmental prediction that as the proportion of direct feeds increases the frequency of aggression will also increase. Over the range of ages studied, senior chicks were not more aggressive during direct feeding bouts than during indirect bouts and rates of aggression did not increase as feeding became increasingly direct. Indeed, if anything, senior chicks attacked more frequently in the early nestling period when fed indirectly than later on when fed directly, although the difference fell short of significance. This result argues against direct feeding being a proximate cue for increased use of aggression. Even if direct feeding is an ultimate cause of broodmate aggression, it seems that direct feeding has little or no proximate influence on use of aggression. Our results suggest that during the period when altricial chicks undergo profound developmental changes in sensory and motor abilities, and in social relations, use of aggression is largely under the control of factors other than feeding method.

Might this evidence against the FMH have been obtained using broods of a size that the hypothesis does not apply to? Broods of two might tend to be better fed and show less aggression and siblicide than the broods of three originally studied by Ploger & Mock (1986), and aggression might become an effective way of competing for food on the floor when there is only one competitor. The idea that two-chick cattle egret broods are too well fed for serious competition to occur did not hold for a previous study with a tropical population where two-chick broods showed significant starvation mortality

(Siegfried, 1972), nor does it apply to our population, where juniors were clearly out competed by seniors, receiving 14.7% less food at the same age. Furthermore, the FMH does not require that aggression be severe enough to lead to siblicide, only that aggression enable privileged access to food (see, for example, Mock & Parker's, 1997, p. 115, application of the hypothesis to the magpie goose, *Anseranas semipalmata*). Finally, total attack rates in our broods (2.18 attacks/h) were 14 times higher than those reported for the dyad with most aggression (2nd and 3rd hatched chicks) in the three-chick broods studied by Ploger & Mock (1986); 1.6 attacks/fight × 1.4 fights/14 h = 0.16 attacks/h. The idea that the hypothesis does not apply to two-chick broods because aggression becomes an effective way of competing for indirect feeds when the number of competitors falls to one is inconsistent with previous claims. For example, it is usually claimed that aggression in two-chick broods of the (direct-feeding) blue-footed booby (*Sula nebouxii*) and some two-chick raptors supports the hypothesis (e.g., Mock et al., 1990). We are not aware of evidence for any species showing that aggression during indirect feeds becomes effective when there is only one competitor.

Our results add to the evidence from studies of pelicans and other ardeids suggesting that aggression is not exclusively associated with direct feeding and not more effective for skewing food allocations during direct than indirect feeding (Milstein et al., 1970; David & Berrill, 1987; Pinson & Drummond, 1993; Ploger & Medeiros, 2004; but see Fujioka, 1985). In sum, descriptive studies of five avian species cast doubt on the suggestion that aggressive exclusion is associated with direct feeding and hence raise doubts as to whether feeding method has a proximate influence on the use of aggression in broodmate feeding competition.

Other hypotheses for development of agonism

If food shortage provokes aggression, rates of aggression should be highest at ages when competition for food is expected to be most acute, and indeed senior chick aggression peaked at the age when estimated food ingestion by the brood also reached its maximum (senior ages when aggression and ingestion peaked: 10.6 ± 1.3 d and 9.9 ± 0.7 d, respectively). Other cattle egret populations have also shown a peak and decline in food ingestion during the nestling period, at variable ages of the senior chick: 20-29 d in a Japanese population observed to age 60 d (Fujioka, 1985) and 10-16 d in a US population observed to age 25 d (Creighton & Schnell, 1996). Similar peaks roughly half-way through the nestling period have been reported in little egrets (*Egretta garzetta*), at 7-11 d (Inoue, 1985), white-tailed tropic birds (*Phaethon lepturus*; Ramos & Pacheco, 2003) and shy albatrosses (*Thalassarche cauta*; Hedd et al., 2002).

We assumed that when food ingestion by the brood is maximal parental work load also peaks and underfeeding becomes more likely. This assumption is supported by senior chick aggression in a Japanese cattle egret population which peaked when food provision to the brood was highest, although this did not occur until age 20-29 d (Fujioka, 1985). Although experimental studies with five different species have demonstrated that a food shortage elicits increased broodmate aggression (review in Drummond, 2001b; Osorno & Drummond, 2003), in ardeids the possible influence of food on aggression is unresolved (Mock et al., 1987a,b; Mock & Lamey, 1991; Creighton & Schnell, 1996; Drummond, 2001b). Our indirect and correlational evidence merely shows that Food Amount is a viable candidate explanation for the observed temporal pattern in aggression.

Dominance was established in all broods by violent pecking and biting, and establishment of dominance could account for the early onset, peak and subsequent decline in agonism. Senior chicks began attacking their broodmates when 6.3 d old and their rate of aggression peaked four days later. Juniors violently resisted the establishment of a dominance-subordination relationship, pecking back when attacked and even initiating fights at ages as young as 4 d (cf., Fujioka, 1985). All three measures of junior chick rebelliousness peaked at average senior chick ages 9.5-10.5 d. Some fights ended when a submissive display by junior chicks (not quantified) appeared to inhibit attacking by seniors: crouching with neck stretched horizontally on the nest floor. When attacks were particularly violent, submissive chicks sometimes flapped their wings while crouching. All of these observations are in accordance with early establishment of a dominance–subordination relationship of the aggression–resistance type (Drummond, 2006), followed by relaxation after successful establishment. In particular, the almost simultaneous decrease in both senior chick rate of aggression and junior rebelliousness at about age 8-10 d, along with the presence of submissive displays, strongly suggests that dominance–subordination relationships were established. This pattern coincides with a previous report of intense aggression in cattle egret broods early in the nestling period, which decreased after the establishment of the hierarchy (Mock & Lamey, 1991).

The Early Dominance Establishment hypothesis may shed light on the surprising result that aggression during feeding did not appear to influence the proportion of food ingested by the senior chick. Early aggression in ardeids seldom increases the proportion of food ingested by the senior chick in the current feeding bout and its main function may well be to establish dominance and secure priority in feeding and survival over the rest of the nestling period (Mock & Parker, 1997; Pinson & Drummond, 1993). After dominance is established, little or no aggression may be necessary to elicit submission or hesitation by juniors during feeding bouts (Mock, 1985; Ploger & Mock, 1986).

Mock (1985) suggested that selection should favour the use of aggression early in the nestling period to establish dominance–subordination relationships, so that seniors can reap the benefits of early aggression when feeding eventually becomes direct. This idea parallels what is proposed by the Early Dominance Establishment hypothesis but it was based on the assumption that aggression is efficient only during competition for direct feeds. According to this view, early aggression would only be adaptive in species with direct feeding or with an eventual switch to direct feeding. However, great blue herons and grey herons that are indirectly fed throughout the nestling period nonetheless present fierce aggression causing wounding or expulsion from the nest (Milstein et al., 1970; Mock, 1985; David & Berrill, 1987), and our analysis of the effects of aggression on competition under direct and indirect feeding suggests that securing priority during direct feeding bouts need not be the main function of nestling aggression.

Our data fail to support the basic assumption that aggression is a more efficient tactic for competing for direct feeds than indirect feeds and they contradict the hypothesis that feeding method has a proximate influence on use of aggression. The cattle egrets' developmental changes in rates of aggression were better predicted by both the Food Amount and Early Dominance Establishment hypotheses. The Food Amount hypothesis is the less plausible of the two hypotheses because it appears unable to explain temporal variation in aggression in blue-footed boobies, where food provisioning continues to increase for at least 10 d after aggression peaks and declines (Guerra & Drummond, 1995; Valderrábano et al., in press) and because the applicability of the hypothesis to ardeids is unresolved. It is the Early Dominance Establishment hypothesis that most credibly explains temporal variation in rates of senior chick aggression in both blue-footed boobies and cattle egrets and also the temporary belligerence and eventual subordination of junior chicks.

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