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ORIGINAL ARTICLE

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Is obligate siblicidal aggression food sensitive?

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Abstract In avian species whose chicks show facultative siblicide, attacks increase with food deprivation. In species that show obligate siblicide, this causal relationship is not expected, but no test has been made. When we composed artificial pairs of young brown boobies, *Sula leucogaster* (an obligately siblicidal species), and supplied variable amounts of food to the older nestlings in each pair, food ingestion was related to the most intense form of attack, pushes, which can cause death by expelling the broodmate from the nest. The less food an older nestling ingested, the more time it spent active and the greater its rate and absolute frequency of pushes, and the more often it expelled its nestmate. Hence, deficient food provision to older nestlings could precipitate siblicidal expulsion of broodmates. Younger nestmates were aggressive too, and the more they were pushed and expelled, the more they pecked. Aggression of senior brown-booby broodmates may be flexible and food sensitive in order to optimize the timing of siblicide or to make siblicide weakly facultative.

Keywords Siblicidal aggression · Brood reduction · *Sula leucogaster*

Introduction

In many avian species where broodmates compete aggressively for parentally provided food, dominant chicks commonly intensify attacking when their individual rate of food ingestion falls. This relationship, formalized as the Food Amount Hypothesis (FAH; Mock et al. 1987; Drummond 2001a), has now been experimentally confirmed for the blue-footed booby (*Sula nebouxii*), the black-legged kittiwake (*Rissa tridactyla*), the osprey (*Pandion haliaetus*), and the black guillemot (*Cepphus grylle*; Drummond and García-Chavelas 1989; Irons 1992; Machmer and Ydenberg 1998; Cook et al. 2000), and may be widely applicable to those species in which aggressive brood reduction is facultative. In facultatively siblicidal egrets and herons, several descriptive and experimental studies consistently failed to support the FAH (Mock et al. 1987; Mock and Parker 1997), but even for this family (Ardeidae) there is evidence (e.g. Creighton and Schnell 1996) that aggression of dominant brood members intensifies with food deprivation (Drummond 2001a, 2001b).

Certainly, it makes ecological sense for animals competing for food to allow food itself to proximately influence how hard they compete, and to aggressively eliminate competitors when food is currently in short supply. Birds may not be alone in this, as behavioural and ecological correlations increasingly point to food shortage as a major factor eliciting intensified fighting between spotted-hyaena littermates (*Crocuta crocuta*; Smale et al. 1995; Golla et al. 1999; Wachter et al. 2002). But there has been no test of whether food amount influences aggression in obligate brood reducers: those avian species whose elder chicks nearly always kill their younger siblings (Anderson 1990a). It has been proposed (e.g. Forbes and Mock 1996) that chicks of such species may not adjust their aggressiveness to the current level of food availability or to their own recent amount of food ingestion.

Food-sensitive aggression would seem inappropriate in obligate brood reducers if, as is widely assumed, parents are usually unable to provision the full brood of two chicks through to independence, and the second egg is laid to insure against possible failure of the first egg/chick (Dorward 1962; Cash and Evans 1986; Clifford and

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Anderson 2001). On this view, both elder chick and parents benefit from elimination of the second chick as soon as survival of the first chick is assured (Evans 1996). Early elimination of a nestling is thought to be adaptive even when there is a current glut of food (Stinson 1979; Forbes 1990; Forbes and Ydenberg 1992) because as food needs inevitably increase with age, parental provision to the brood will eventually become inadequate. In line with this thinking, descriptive information is broadly consistent with aggression in obligately siblicidal species being unconditional: survival of junior brood members is rare; death generally occurs in the 1st week of life, and the severity of pecking, biting, and pushing often seems maximal, even when parents are apparently providing abundant food (Meyburg 1977; Gargett 1978; Gerhardt et al. 1997).

However, most behavioural data on obligately siblicidal species are somewhat anecdotal and there has been no attempt to formally relate intensity of aggression to amount of food ingested by the aggressor, either descriptively or experimentally. Furthermore, some authors have speculated that when obligate brood reducers occasionally raise two chicks to fledging, this could represent an adaptive response to favourable breeding conditions. Flexible control of mortality could reside in parents, who might thwart siblicide by facultatively reducing the asymmetry in age and size of broodmates (Simmons 1988), or it could reside in the chicks themselves, who might reduce their aggression when well fed (Tershey et al. 2000).

The brown booby (*S. leucogaster*) lays clutches of one or two eggs but seldom raises two chicks to fledging; when both eggs hatch, the older chick normally kills its nestmate within several days (reviews in Dorward 1962; Nelson 1978). Violent pecking and pushing by the older chick quickly leads to death by starvation or expulsion, so that within a week of hatching, 65% of younger chicks on San Pedro Mártir Island and all younger chicks on Isla Isabel (where chicks are heavily predated) were dead (Cohen Fernández 1988; Tershey et al. 2000). These figures suggest that most older chicks cause their sibling's death while themselves only 5–12 days old. On Johnston Atoll, 1.4% of all clutches (Amerson and Shelton 1976), and on Isla San Pedro Mártir, 7% of two-egg clutches produced two fledglings each, leading Tershey et al. to propose that siblicide in the latter population may be facultative. However, according to the widely accepted criterion of Simmons (1988), siblicide may be obligate in all populations of brown boobies described so far, since in every study it seems that fewer than 10% of junior chicks survived.

We tested applicability of the FAH to an obligately siblicidal species by applying different levels of food deprivation to the older members of artificially composed two-chick broods of brown boobies. We used chicks that were several days older than the age when siblicide usually occurs, in order to work with subjects mature enough to be artificially fed and temporarily installed in observation nests where no brooding was available. Experiments and observations have shown that aggression of obligate brood reducers potentially persists well beyond the age when siblicide normally occurs (Steyn 1973; Anderson 1990b; review in Drummond 2001b), and on Isla San Pedro Martir, pairs of brown-booby broodmates that naturally survived to age 4–9 weeks were highly aggressive (Drummond et al. 2003).

Additionally, we described the aggressive behaviour of the younger nestmate. The FAH generates no prediction for the behaviour of younger nestmates in our trials (their food consumption was not manipulated), but we analysed their behaviour to gain understanding of the behavioural dynamics between nestmates of an obligate brood reducer. Behaviour of younger nestmates of obligate brood reducers is virtually unknown because they usually die so young. When experimentally paired with blue-footed boobies that were 5.5 days older, brown boobies proved to be highly aggressive despite their substantial age-related disadvantage in size and maturity, and they also showed great unexplained individual variation in their aggressiveness (Drummond et al. 2003). Therefore, we asked how aggressive brown boobies would be when paired with older conspecifics, and whether in our experimental context younger chicks would modify their aggressiveness in response to possible food-related variation in aggressiveness of their nestmates.

Methods

The study population is a colony of brown boobies on Isla Larga, a 41.2-ha island in the Islas Marietas group of islands at the mouth of Bahía de Banderas (105°36′N, 20°43′W), on the Pacific coast of Mexico (Grant 1964; Rebón-Gallardo 2000). We inspected 550 nests during the period 23 July to 2 August 2001, to detect (unsexed) singleton chicks that could be paired with other singletons to form experimental dyads. Most were probably singletons from the time of hatching, but a substantial minority were probably survivors (mostly a-chicks) from reduced two-chick broods. Random assignment of subjects to experimental treatments prevented differences in early experience generating correlations between food ingestion and aggressive behaviour. The 24 dyads we formed comprised older chicks of age 16.8±0.33 days (mean±SE) and younger chicks of age 12.0±0.31 days, and the within-dyad age difference was 4.8±0.18 days, similar to the value for natural broods (4.6±0.17 days, Cohen Fernández 1988). Ages were estimated on the day each chick was first found, using known age/culmen-length curves of brown boobies measured on Isla Isabel, Nayarít, México.

The older chick of each dyad was randomly assigned to 1 of 12 artificial feeding levels (treatments), representing 11 equal increments from 0% to 110% of the estimated natural 24-h food intake for a chick of its own age. The estimates were based on Guerra and Drummond's (1995) field estimates of ingestion during the 24-h day by senior chicks in natural two-chick broods of the slightly larger blue-footed booby. They are not likely to be overestimates, because in that study, the weight of chicks was 8.8% lower than that of controls, due to repeated handling that presumably depressed their food intake. There was no association between assigned treatment and the magnitude of the asymmetry on day 1 between dyad members [(older-younger)/older] in bodyweight (r_S=0.025, P=0.91, N=24) or culmen length (r_S=–0.031, P=0.89, N=24). Originally, there were 26 dyads, assigned as equally as possible to the 12 treatments, but 2 dyads were deleted from the sample because a chick disappeared from its natal nest before the end of the experiment. The artificial food was whole sardine canned in water. The brown booby's natural diet includes flying fish and squid, as well as many other species of fish (Nelson 1978), and in the Mexican Pacific Ocean includes sardines (personal observation). Mushy fragments of sardine of <4 cm^3 were inserted into a chick's mouth after gently opening its mandibles with the fingers, and the fragments were promptly and readily swallowed. Successive fragments were inserted until the feed was complete. Chicks assigned the 0% treatment were sham-fed, following the same routine of capture, mouth opening and (feigned) insertion.

To control for individual variation, which can be considerable in this species (Drummond et al. 2003), the rate or frequency of aggression of each older chick was measured at baseline (after natural parental care) and again after experimental treatment. We first withdrew the two chicks from their respective natal nests on day 1 at 1740 hours, weighed and measured (culmen length) them, and marked their heads and rumps with a spot of red (older chick) or blue (younger chick) paint for individual recognition. Then we inserted the two chicks simultaneously into an abandoned brown-booby nest (roughly reconstructed into the shape of an occupied nest) at 1800 hours and recorded their behaviour for 30 min (baseline scores). At this time of day the thermal environment was comfortable for unbrooded chicks. Next we gave each older chick its first of three feeds and then fastened micropore tape around its neck to prevent ingestion of parental feeds during the next 23 h. We returned both chicks to their respective natal nests, where we watched for 5 min to confirm acceptance by the parents (which always happened immediately). If no parent was initially present, we waited until it arrived. The tape was not tight and did not cause any visible damage to skin or down, or elicit behaviour indicating discomfort (Drummond and García-Chavelas 1989), but the tape largely prevented the neck expanding to permit the passage of parentally provided food. The next two feeds were provided to each older chick during brief removal from the natal nest at 0700 hours and 1200 hours on day 2, and for each of these feeds the tape was temporarily removed. The three equal feeds summed to the assigned age-specific percentage of artificial food. Three chicks regurgitated the artificial food on one occasion each, and for the purpose of analysis, we discounted the regurgitated masses from their assigned percentages of food intake. The younger member of each dyad, which was not fitted with tape, fed normally from its parents between the observations of day 1 and day 2. Finally, at 1740 hours on day 2, we withdrew the two dyad members from their natal nests, weighed and measured them, removed the tapes of the older chick, and at 1800 hours observed them again for 30 min in the abandoned nest where they were first observed. Afterwards, both chicks were permanently reinstalled in their natal nests, where in every case we confirmed their continued presence over the next few days.

The increase in bodyweight of older chicks during the day of artificial feeding was correlated with the percentage of food provided (r=0.331, P=0.057, N=24, one-tailed Pearson's correlation), suggesting that the experimental treatments successfully manipulated the amount of food ingested between observations. The weakness of this correlation may be due to bodyweights on day 1 being differentially inflated in different individuals by variable amounts of food in the intestines, and also to older chicks managing to ingest some parentally provided food despite the tapes.

The observer sat 4–6 m from the abandoned nest without a blind, and recorded the absolute frequency of pecks (impact of the bill on the victim), bites (the victim is seized in the mandibles for at least 1 s), pushes (the seized victim is displaced at least 1 cm by thrusting with the mandibles), expulsions (the victim is forced or flees across the perimeter rim of the nest) and submissive postures (bill-down-and-face-away, Nelson 1978). In "expulsion pushes", the aggressor seizes a body part for several seconds while thrusting forcefully forward and upward and, if able, walking forward (Drummond et al. 2003). Expulsion pushes were recorded as bites or pushes, depending on whether the victim's whole body was displaced. Expelled chicks were promptly replaced into the centre of the nest and observation continued. The observer also recorded every half-minute (signalled precisely by a bleep) whether each chick was inactive (head resting on any substrate or invisible under the experimental nestmate) or active in that instant (one-zero sampling). This last record allowed us to estimate the proportion of the time when both pairmates were simultaneously active, in order to calculate behavioural rates.

We tested for negative correlations between treatment (food amount) and behavioural scores on day 2 with Kendall's partial tau coefficient (Siegel and Catellan 1988), using the day 1 behavioural scores as a covariate. Abundant food ingestion could, in principle, depress aggression by inducing somnolence, so we analysed rates of older chick aggressive acts during periods when both chicks were active, which is a measure of their aggressiveness. We also analysed absolute frequencies of aggressive acts during the whole 30-min trial, a variable that integrates both duration of interaction and intensity of aggression and better expresses the impact on the victim. Behavioural data were not normally distributed even after applying the standard transformations, so we were unable to use parametric statistical tests. Each category of aggression (pecks, bites, pushes) was treated as representing an independent null hypothesis; thus no P-value adjustment was used. P-values are conservative in that we report two-tailed probabilities for tests of directional predictions (Rice and Gaines 1994). Sample values are expressed as $\bar{X}$±SE throughout.

Results

Chicks were active most of the time, mainly attacking each other but also crawling about the nest as if seeking a brooding adult. They did not beg. Interaction between them occasionally ceased when a chick rested in prostrate posture or moved away to the rim of the nest. Their agonistic behaviour was qualitatively similar to the behaviour we observed in natural broods of two chicks in the same colony (Fig. 1). All 24 older chicks attacked their experimental nestmates on both days, except 1 older chick that attacked only on the 1st day, and 9 older chicks managed to expel their nestmates 1–8 times. Averaging over the complete observation periods of the 2 days, the 24 older chicks delivered 28.4±5.49 pecks per hour, 71.0±26.22 bites per hour, 17.1±6.84 pushes per hour and 2.1±0.72 expulsions per hour. Of 24 younger chicks, 21

Fig. 1 The senior chick of a natural two-chick brown-booby brood evicts its sibling over the nest rim with an expulsion push

Table 1 Mean (±SE) aggressive acts on day 1 (baseline) and day 2 (after food deprivation of variable intensity) of 24 dyads comprising 1 younger and 1 older nestmate

Chick		Aggressive acts			
		Pecks	Bites	Pushes	Expulsions
Frequency during whole 30-min trial					
Day 1	Older	14.46±3.46	27.61±12.61	3.58±2.19	0.63±0.35
	Younger	6.25±1.93	8.04±4.74	2.75±1.94	0.25±0.25
Day 2	Older	14.46±3.04	40.70±13.40[b]	12.75±4.83*[b]	1.42±0.50[b]
	Younger	4.33±1.41	2.04±0.80	0.00±0.00[a]	0.00±0.00
Rate (events/hour) during time when both nestmates were active					
Day 1	Older	24.64±6.04	42.95±19.74	5.62±3.44	0.99±0.55
	Younger	11.94±4.72	15.13±9.46	6.36±5.21	0.31±0.31
Day 2	Older	25.27±5.80	69.39±26.40[b]	20.68±26.40*[b]	2.18±2.75[b]
	Younger	7.30±2.50	3.50±1.18	0.00±0.00[a]	0.00±0.00

* Day 2>day 1, [a] day 2<day 1, at $P<0.05$; a two-tailed Wilcoxon test compared older chicks on day 1 versus day 2 and younger chicks on day 1 versus day 2.

[b] Significant correlation between treatment (level of food deprivation applied to older chick) and aggressive behaviour of older or younger chick on day 2; Spearman's test, $P<0.05$.

showed aggression, most of them attacking on both days, although attack rates of the 24 younger chicks were roughly 3–8 times lower than those of their larger nestmates: 9.6±2.83 pecks per hour, 9.3±4.66 bites per hour and 3.2±2.60 pushes per hour (and 0.2±0.16 expulsions per hour). Even so, one younger chick managed to expel its nestmate six times, at a time (day 1) when the older chick outweighed it by 32%. Most expulsions involved physical ejection by behaviour recorded as bites and pushes and involving expulsion pushes, but a few victims fled from the nest. Although attacked chicks (including older chicks) frequently turned away and cowered when struck on the head and face, no unambiguous submissive posture was seen; the bill-down-and-face-away posture of the blue-footed booby was rare or absent.

Behavioural rates during simultaneous activity of nestmates and behavioural frequencies during the whole trial, on days 1 and 2, are summarized in Table 1. We tested to confirm that random assignment of treatments (percentages of food) resulted in treatments being independent of levels of aggression at baseline (day 1). There were no associations between treatments and either pushes (frequency: $r_S=-0.089$, $P=0.68$; rate: $r_S=-0.098$, $P=0.65$) or expulsions (frequency: $r_S=-0.266$, $P=0.21$; rate: $r_S=-0.276$, $P=0.19$). However, by chance, treatments were negatively correlated with pecks (frequency: $r_S=-0.327$, $P=0.12$; rate: $r_S=-0.390$, $P=0.06$) and with bites (frequency: $r_S=-0.347$, $P=0.10$; rate: $r_S=-0.404$, $P=0.05$). Our statistical analysis controlled for these chance associations by including behavioural scores on day 1 as a covariate when testing for a correlation between treatment and behavioural scores on day 2.

Older chicks

The proportion of time that the 24 older chicks were active was 0.94±0.02 on day 1 and 0.86±0.04 on day 2. The change from day 1 to day 2 in this proportion was negatively related to the amount of food ingested ($r_S=-0.425$, $N=24$, $P<0.05$): the more food older chicks ingested, the greater their increase in sleeping. Accordingly, it is appropriate to analyse not only absolute frequencies of aggression during the whole 30-min trial but also rates of aggression (events/hour) when both nestmates were active, as planned.

There was a negative relationship between amount of food ingested by older chicks and the rate of the most consequential category of aggression on day 2: holding day 1 scores constant, treatment was not correlated with rate of pecking (tau=–0.13, $N=24$, $P=0.19$) or biting (tau=–0.20, $N=24$, $P=0.09$), but it was negatively correlated with rate of pushing (tau=–0.39, $N=24$, $P<0.005$; Fig. 2). That is, the less we fed older chicks, the greater their subsequent rate of pushing. The 12 older chicks that received no more than 50% of the normal amount of food increased their pushing when both nestmates were active by an average 26.3±10.3 pushes per hour, above their baseline rate of 10.41±6.7 pushes per hour (Fig. 2). Analysis of the frequencies (during the whole trial) of aggressive behaviours on day 2 showed a similar pattern to the analysis of rates when nestmates were simultaneously active (pecks: tau=–0.16, $N=24$, $P=0.14$; bites: tau=–0.22, $N=24$, $P=0.07$; pushes: tau=–0.39, $N=24$, $P<0.005$).

Five of the 12 older chicks that received no more than 50% of the normal amount of food did not increase their pushing or did so minimally (Fig. 2). Four of these did not push on either observation day and the other pushed just four times on day 2, implying that these individuals were relatively unaggressive in our testing situation. Interestingly, their younger nestmates were also relatively unaggressive, giving only 7.2+4.42 pecks on day 1 compared to 52.0+14.52 pecks by younger nestmates of the other 7 older chicks that were severely underfed.

On day 2, both the rate of expulsions of younger nestmates (tau=–0.31, $N=24$, $P<0.02$) and the frequency of expulsions of younger nestmates (tau=–0.31, $N=24$, $P<0.02$) were correlated with amount of food ingested by

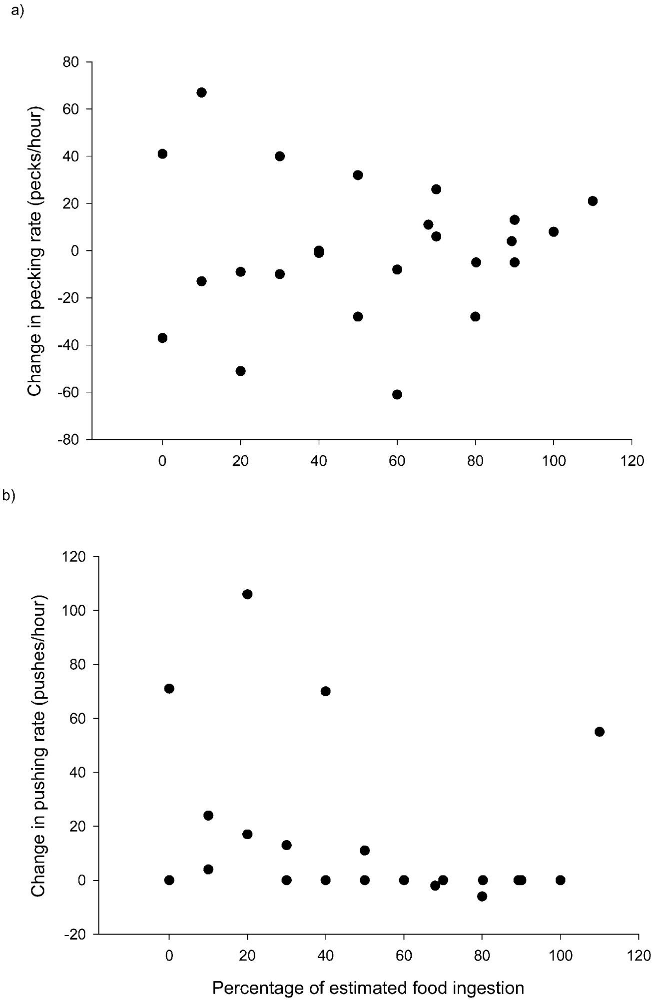

Fig. 2a, b Relationship between amount of food ingested by 24 older chicks and subsequent change (day 2 minus day 1) in their rates of **a** pecking, and **b** pushing. We show change in behaviour to control for differences in aggressiveness of individual chicks, present on day 1

the older chick, when day 1 scores were held constant. The greater its food deprivation, the more often did a chick expel its younger nestmate.

Younger chicks

We analysed the relationship between the behaviour of younger and older chicks on day 2 (without taking day 1 into account). The rate of pecking by younger chicks on day 2 was not related to the older nestmate's rate of pecking (r_S=0.127, N=24, P=0.55) or biting (r_S=0.250, N=24, P=0.24), but it was positively correlated with that nestmate's rate of pushing (r_S=0.404, N=24, P<0.05) and expelling (r_S=0.414, N=24, P<0.05). The more intensely they were pushed and expelled by their nestmates, the more intensely younger chicks pecked their nestmates. A similar pattern of correlations was found between absolute frequency during the whole trial of pecking by younger chicks (on day 2) and absolute frequencies of aggressive behaviours by older chicks (pecking: r_S=0.303, N=24, P=0.15; biting: r_S=0.323, N=24, P=0.12; pushing: r_S=0.468, N=24, P<0.02; expelling: r_S=0.495, N=24, P<0.02).

(By contrast, on day 1, there was no association between the pecking behaviour of younger chicks and any aggressive behaviour of older chicks: pecking: r_S=0.338, N=24, P=0.11; rate of pecking: r_S=0.340, N=24, P=0.10; biting: r_S=0.00, N=24, P=0.99; rate of biting: r_S=0.027, N=24, P=0.90; pushing: r_S=0.140, N=24, P=0.52; rate of pushing: r_S=0.158, N=24, P=0.46; expelling: r_S=0.291, N=24, P=0.17; rate of expelling: r_S=0.318, N=24, P=0.13.)

Discussion

Behaviour of older chicks

Although absence of an adult in the experimental nests made chicks restless, our protocol evidently allowed the expression of agonistic behaviour similar to the intense aggression which in natural circumstances results in hatchling siblicide (cf. Cohen Fernández 1988). Older chicks emitted an average of 116 aggressive acts per hour, mostly involving sustained seizing, and often with sufficient force to result in displacement and expulsion of the younger nestmate. We can only generalize confidently from our sample to senior chicks of similar age (roughly 17 days), but we note that this is not much greater than the ages (5–12 days) at which most natural siblicide seems to be perpetrated (Cohen Fernández 1988; Tershey et al. 2000). It seems likely that the demonstrated sensitivity of aggressive behaviour to recent food ingestion is also prevalent at the younger ages when senior chicks normally expel their broodmates, although the magnitude of the effect could vary with age. It is also worth noting that the social experience of our subjects was different from that of brown-booby seniors and juniors in the normal competitive situation, in that they either grew up as singletons or (in a probable minority of cases) experienced early loss of a nestmate. Early experience cannot account for the significant correlations we report because experimental treatments were assigned randomly to individual subjects, and therefore were not associated with early experience. However, we cannot completely discount the unlikely possibility that sensitivity of aggressiveness to food ingestion is prevalent only in chicks confronted by novel nestmates or inserted into unfamiliar nests.

Food deprivation caused older chicks to remain active during a greater proportion of the time and also to be more aggressive when active. Conversely, there was no evidence that ingestion of the highest food provision reduced aggressiveness, and it is tempting to conclude that abundant food ingestion does not assuage aggressiveness. However, there are two reasons for keeping an open mind on the possible effects of abundant food provision. First, it is doubtful that our highest food provision satiated chicks at the time of observations, which occurred 6 h after the last artificial feed. Second, when Cohen Fernández (1988) watched 13 brown-booby broods 24-h/day from hatching to death of the junior chick (before age 7 days), she noted qualitatively that senior broodmates generally desisted from aggression when they were satiated, as evidenced by them ceasing begging and declining parental food offers.

Importantly, older chicks that consumed 50% or less of the estimated normal 24-h food allocation more than doubled their rate of pushing but did not bite or peck more than better-fed chicks. That is, food deprivation had little effect on the high baseline level of attacking, but elicited intensification of the expulsive component: blows by hungry chicks may not have been more frequent overall, but were more likely to be sustained beyond impact and seizing to the point where the nestmate was physically displaced. Senior brown-booby chicks respond to underfeeding by doing more expulsion pushing. A minority of the underfed seniors showed little or no pushing on either observation day, associated with little aggression by their nestmates, but their relative pacifism could have been induced by transfer into a novel nest with no brooding adult.

Food deprivation increased the probability of siblicide by precipitating more frequent expulsions. In the natural situation, brooding parents may impede broodmate hostilities, accidentally or otherwise, making eviction of younger broodmates more difficult than in the experiment. Even so, intensified expulsion pushing should hasten siblicide unless parents respond to intensification by defending their younger offspring. Parents of obligate siblicide species apparently do not defend their younger chicks against aggressive expulsion (e.g. Lougheed and Anderson 1999), but it is worth noting that, in principle, brown-booby parents could provide limited protection by ensuring their elder chicks are not deprived of food.

It is instructive to contrast the food sensitivity of the obligately siblicidal brown booby with that of the facultatively siblicidal blue-footed booby. Food-deprived blue-footed boobies attacked several times more frequently than usual, but they did not physically evict their broodmates (Drummond and García-Chavelas 1989). Indeed, expulsion pushing is rare or absent in blue-footed boobies, and when junior chicks depart the nest they usually do so under their own steam after suffering starvation combined with violent pecks and bites (personal observation). Agonism by blue-footed booby chicks, which is often expressed by ritualized displays, establishes dominance and secures feeding priority, and only occasionally results in death of the broodmate. By contrast, in obligately siblicidal species (including the brown booby) agonistic displays seem to be absent, and the main function of aggression is to kill the broodmate by expulsion, starvation and lesions (Drummond 2001b). Thus reduced ingestion induces each species to intensify what it ordinarily does: blue-footed boobies increase their aggressive domination whereas brown boobies more quickly expel their broodmates. The other three facultatively siblicidal species that have been experimentally tested for effects of food deprivation all increased their rates of attacking (reviewed in Drummond 2001a), similar to the blue-footed booby.

But why is the aggression of an obligately siblicidal species condition-dependent at all? If the function of brown-booby aggression is to kill, why not simply show maximal aggression in all circumstances? It seems unlikely that food sensitivity is a vestige, retained from a facultatively siblicidal ancestor (such as the blue-footed booby), because the ancestral form was probably a species that laid a single-egg clutch (plausibly the red-footed booby, *S. sula*; Friesen and Anderson 1997). We consider four functional hypotheses to explain why the baseline level of brown-booby aggression is submaximal and why intensification occurs when food ingestion declines.

First, facultative food-dependent aggression could be a mechanism by which the senior chick optimizes the timing of its broodmate's death. Timing of the junior chick's death can have important consequences for the senior chick (Forbes 1990). Maximal aggression might prematurely kill junior, the back-up chick that potentially provides insurance coverage for loss of senior through predation or developmental failure. Hence, we should expect the senior chick's aggression to be set at an intensity that allows junior to survive until the age when the cost of cohabiting with it becomes unacceptably high. The cost of cohabiting should rise steeply as the junior chick approaches the age/size where it could evade or thwart siblicidal attacks or attempt siblicide itself. In this scenario, the senior chick may need to abandon restraint at an earlier age than usual if parents are bringing insufficient food to currently sustain two chicks, or if its broodmate is receiving too great a share of parental food (and consequently may soon become unkillable or uncontainable). In either of these circumstances, the senior chick would be poorly fed by parents and could respond by urgently expelling the broodmate, to head off personal starvation or siblicidal attacks by junior. Certainly, junior chicks of obligate siblicide species are sometimes killed or rendered inviable by broodmate aggression before the age when the insurance coverage they provide becomes redundant (Anderson 1990b; Evans 1996, 1997), and their hasty expulsion is plausibly explained by the senior chicks' need to eliminate potentially lethal rivals (Drummond et al. 2003; but see alternative interpretation of ages of junior-chick death in Evans 1996, 1997).

Second, submaximal aggression may open the door to occasional siblicidal substitution of a weak senior chick by a vigorous and more valuable junior chick. Clearly such "progeny choice" (Forbes 1991; Forbes and Mock 1998) could benefit parents, but it seems unlikely that it would benefit a senior chick unless the senior chick's sacrifice were compensated by the survival of a markedly superior full sibling. In a similar context, O'Connor (1978) dismissed suicidal self-sacrifice by most junior broodmates of facultative siblicide species as unlikely to evolve.

Third, condition-dependent aggression may occasionally secure an indirect fitness benefit by allowing both broodmates to fledge when food is abundant (Tershey et al. 2000); that is, brown-booby siblicide may be weakly facultative rather than truly obligate. Certainly, in other populations (and possibly in Las Marietas), both brown-booby broodmates sometimes survive at least until they are nearly fully feathered (Amerson and Shelton 1976; Tershey et al. 2000), although we do not know whether such birds fledge at normal size and mass nor whether they manage the transition to independence and recruitment into the breeding population. When obligately siblicidal Nazca boobies (*S. dactylatra*) were prevented from killing their broodmates, some parents were able to raise two-chick broods more than half way to fledging (Anderson 1990b), but these chicks were undersized and may not have fared well subsequently. The fierce and usually lethal aggression of senior brown-booby chicks seems inconsistent with siblicide being facultative, but the aggression may vary more than we think. In the absence of adequate quantification of aggression in any obligately siblicidal species, we simply do not know how much aggression varies among individuals and with circumstances. Also, if junior chicks are desperados that potentially threaten the survival of senior chicks (Drummond 1993; Drummond et al. 2003), seniors would be obliged to maintain a high level of aggression to contain that threat. Even when seniors stand to benefit from their siblings' survival, they might err on the side of siblicide rather than placing their own lives in unacceptable jeopardy.

Fourth, the important functional context for the expression of food-sensitive aggression may not be senior-chick aggression but junior-chick aggression. Some, but not all, junior brown boobies fostered into blue-footed booby nests relentlessly attacked their larger (blue-footed booby) nestmate, in two cases even to the point of successfully subduing it or expelling it from the nest (Drummond et al. 2003). In natural broods on Isla Isabel, prior to their expulsion, junior brown boobies received roughly 4–10 times fewer parental feeds than their broodmates (Drummond 2002), implying that severe food deprivation is normal for junior chicks of this species. Yet the occasional survival of both brown-booby broodmates implies that in some situations, possibly when their food ingestion is relatively high, it could be adaptive for juniors to moderate their attacks. Here again, there may be scope for selection on the behaviour of the habitual underlings (junior chicks) to drive the evolution of agonistic behaviour.

Behaviour of younger chicks

The non-submissive, highly aggressive and potentially lethal behaviour observed in younger brown-booby nestmates supports the prediction of the desperado sibling hypothesis: junior chicks of obligately siblicidal species, instead of learning a subordinate role, should struggle violently to overcome and kill their (larger) rivals (Drummond 1993; Drummond et al. 2003). Despite being exposed to almost continuous harrassment, younger chicks performed an average of 22 aggressions per hour (on days 1+2), most of which involved sustained seizing of the larger nestmate. Many of these attacks were sufficiently forceful to displace the nestmate, some even ousting it from the nest. The occurrence and efficacy of this aggression were not artifacts of our protocol; Cohen Fernandez (1988) observed a 5.5-day-old junior chick in a natural brown-booby brood expel its elder sibling from the nest (although it re-entered a few minutes later).

Intriguingly, on day 2 (only), it was the younger chicks suffering most pushing and expulsion (by rate or frequency) that themselves performed the most pecking (by rate or frequency). Younger chicks were not exposed to food deprivation, so this elevated pecking was almost certainly provoked by the behaviour of the older nestmates. Intensified pecking could be a functional response: in extremis, juniors may make their utmost effort to frustrate attacks or to kill their attacker. It was the highly threatening pushing, rather than mere pecking and biting, that provoked this extreme effort. Evidently, the aggression of junior brown-booby chicks is normally submaximal, implying some constraint on their attempts to expel their assailants. Possibly juniors ordinarily withhold some aggression to avoid provoking increased attacking by broodmates, or juniors may sometimes save their energy to avoid debilitation. Tellingly, 21% of white-pelican juniors whose elder siblings were experimentally removed from the nest were already so debilitated by sib attacks at ages 3 days or 6 days, that they were unable to substitute successfully for their siblings (Evans 1996, 1997).

The aggression of brown-booby chicks, seniors and juniors may turn out to involve more flexibility and contingency than we have hitherto suspected, and the same may hold for other obligately siblicidal species.

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References

Amerson BA, Shelton PC (1976) The natural history of Johnston Atoll, Central Pacific Ocean. Atoll Res Bull 192:213–235

Anderson DJ (1990a) Evolution of obligate siblicide in boobies. I. A test of the insurance-egg hypothesis. Am Nat 135:334–350

Anderson DJ (1990b) Evolution of obligate siblicide in boobies. II. Food limitation and parent-offspring conflict. Evolution 44:2069–2082

Cash KJ, Evans RM (1986) Brood reduction in the american white pelican (*Pelecanus erythrorhynchos*). Behav Ecol Sociobiol 18:413–418

Clifford LD, Anderson DJ (2001) Experimental demonstration of the insurance value of extra eggs in an obligately siblicidal seabird. Behav Ecol 12:340–347

Cohen Fernández EJ (1988) La reduccion de la nidada en el bobo café (*Sula leucogaster nesiotes* Heller and Snodgrass 1901). Thesis, Universidad Nacional Autónoma de México

Cook MI, Monaghan P, Burns MD (2000) Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling black guillemots *Cepphus grylle*. Behav Ecol 11:282–287

Creighton JC, Schnell GD (1996) Proximate control of siblicide in cattle egrets: a test of the food amount hypothesis. Behav Ecol Sociobiol 38:371–377

Dorward EF (1962) Comparative biology of the white booby and brown booby, *Sula* spp. at Ascension. Ibis 103b:174–220

Drummond H (1993) Have avian parents lost control of offspring aggression? Etología 3:187–198

Drummond H (2001a) A revaluation of the role of food in nestling aggression. Anim Behav 61:1–10

Drummond H (2001b) The control and function of agonism in avian broodmates. In: Slater PJB, Rosenblatt JS, Snowdon CT, Roper TJ (eds) Advances in the study of the behavior. Academic, New York, pp 261–301

Drummond H (2002) Begging versus aggression in avian broodmate competition. In: Wright J, Leonard ML (eds) The evolution of begging: competition, cooperation and communication. Kluwer, Dordrecht, pp 337–360

Drummond H, García-Chavelas C (1989) Food shortage influences sibling aggression in the blue-footed booby. Anim Behav 37:806–819

Drummond H, Rodríguez C, Vallarino A, Valderrábano C, Rogel G, Tobón E (2003) Desperado siblings: uncontrollably aggressive junior chicks. Behav Ecol Sociobiol 53:287–296

Evans RM (1996) Hatching asynchrony and survival of insurance offspring in an obligate brood-reducing species, the american white pelican. Behav Ecol Sociobiol 39:203–209

Evans RM (1997) Parental investment and quality of insurance offspring in an obligate brood-reducing species, the american white pelican. Behav Ecol 8:378–383

Forbes LS (1990) Insurance offspring and the evolution of avian clutch size. J Theor Biol 147:345–359

Forbes LS (1991) Insurance offspring and brood reduction in a variable environment: the costs and benefits of pessimism. Oikos 62:325–332

Forbes LS, Mock DW (1996) Food, information and avian brood reduction. Ecoscience 3:45–53

Forbes LS, Mock DW (1998) Parental optimism and progeny choice: when is screening for offspring quality affordable? J Theor Biol 192:3–14

Forbes LS, Ydenberg RC (1992) Sibling rivalry in a variable environment. Theor Popul Biol 41:335–360

Friesen VL, Anderson DJ (1997) Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. Mol Phylogen Evol 7:252–260

Gargett V (1978) Sibling aggression in the black eagle in the Matopos, Rhodesia. Ostrich 49:57–63

Gerhardt RP, Gerhardt DM, Vásquez MA (1997) Siblicide in swallow-tailed kites. Wilson Bull 109:112–120

Golla W, Hofer H, East ML (1999) Within-litter aggression in spotted hyaenas: effect of maternal nursing, sex and age. Anim Behav 58:715–726

Grant PR (1964) The birds of the Tres Marietas Islands, Nayarít, Mexico. Auk 81:514–519

Guerra MC, Drummond H (1995) Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. Behaviour 132:479–496

Irons DB (1992) Aspects of foraging behavior and reproductive biology of the black-legged kittiwake. PhD Thesis, University of California, Irvine

Lougheed LW, Anderson DJ (1999) Parent blue-footed boobies suppress siblicidal behavior of offspring. Behav Ecol Sociobiol 45:11–18

Machmer MM, Ydenberg RC (1998) The relative roles of hunger and size asymmetry in sibling aggression between nestling ospreys *Pandion haliaetus.* Can J Zool 76:181–186

Meyburg BU (1977) Sibling aggression and cross-fostering of eagles. In: Temple SA (ed) Endangered birds. University of Wisconsin Press, Madison, pp 195–200

Mock DW, Parker GA (1997) The evolution of sibling rivalry. Oxford University Press, London

Mock DW, Lamey TC, Williams CF, Ploger BJ (1987) Proximate and ultimate roles of food amount in regulating egret sibling aggression. Ecology 68:1760–1772

Nelson JB (1978) The Sulidae: gannets and boobies. Oxford University Press, London

O'Connor RJ (1978) Brood reduction in birds: selection for fraticide, infanticide, and suicide. Anim Behav 26:79–96

Rebón-Gallardo F (2000) Distribución, abundancia y conservación de la avifauna de las islas Marietas, Nayarit, México. An Inst Biol Univ Nac Auton Mex Ser Zool 71:59–88

Rice WR, Gaines SD (1994) "Heads I win, tails you lose": testing directional alternative hypotheses in ecological and evolutionary research. Trends Ecol Evol 6:235–237

Siegel S, Catellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Simmons R (1988) Offspring quality and the evolution of cainism. Ibis 130:339–357

Smale L, Holekamp KE, Weldele M, Frank LG, Glickman SE (1995) Competition and cooperation between litter-mates in the spotted hyaena, *Crocuta crocuta*. Anim Behav 50:671–682

Steyn P (1973) Observations on the tawny eagle. Ostrich 44:1–23

Stinson CH (1979) On the selective advantage of fratricide in raptors. Evolution 33:1219–1225

Tershey BR, Breese D, Croll DA (2000) Insurance eggs versus additional eggs: do brown boobies practice obligate siblicide? Auk 117:817–820

Wachter B, Honer OP, East ML, Golla W, Hofer H (2002) Low aggression levels and unbiased sex ratios in a prey-rich environment: no evidence of siblicide in Ngorongoro spotted hyenas. Behav Ecol Sociobiol 52:348–356