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The function of hatching asynchrony in the blue-footed booby

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Abstract The blue-footed booby (*Sula nebouxii*) commonly hatches two eggs 4 days apart; then the senior (first-hatched) chick aggressively dominates the other and sometimes kills it. Two hypotheses explaining the function of the hatching interval were tested by creating broods with synchronous hatching: the facultative brood reduction hypothesis of Lack (1954) and the sibling rivalry reduction hypothesis of Hahn (1981). The results contradicted most predictions of both hypotheses: synchronous broods formed an aggressive hierarchy similarly to asynchronous broods (controls), and subordinate chicks grew poorly (Fig. 1) and died frequently, similarly to junior chicks in control broods. However, compared with synchronous broods, asynchronous broods showed less aggression (Fig. 2), diminished food allocation to subordinate chicks (Fig. 3) and less total food consumption (30% fewer feeds at age 0–10 days). These behavioral comparisons took into account the different ages of chicks in different treatments. The results suggest that natural asynchrony makes brood reduction more efficient and decreases the costs of sibling aggression to parents, in terms of their future survival or fecundity, as proposed by Mock and Ploger (1987). Further, in exaggeratedly asynchronous broods (8-day hatch interval) junior chicks suffered more aggression (Fig. 4) and grew more slowly than junior chicks in control broods. This result supports the hypothesis of optimal hatch asynchrony of Mock and Ploger (1987).

Key words Hatching asynchrony · Function · Booby

Introduction

The most widely cited explanation of asynchronous hatching in birds is the facultative brood reduction hypothesis of Lack (1947, 1954, 1966, 1968) (but see Clark and Wilson 1981; Amundsen and Stokland 1988, Lessells and Avery 1989). Despite confirmation of this hypothesis in an experimental study of a single species (Magrath 1989), doubts persist over the validity of the hypothesis or the generality of its application. Amundsen and Stokland (1988) concluded that the brood reduction hypothesis does not explain asynchrony because most experimental studies failed to show that synchronous broods produce fewer or smaller offspring.

According to the facultative brood reduction hypothesis, staggered hatching permits parents to adjust brood size to unpredictable food resources by efficiently eliminating extra chicks when feeding conditions turn out to be poor during the raising of the brood. Competitive asymmetries between broodmates, due initially to differences in age, allow the elder ones to control food allocation and assure their own food supply; younger ones starve if the left-overs are not sufficient. Effectively, junior brood members die promptly in lean years so that seniors can fledge at a viable size and mass; if this did not happen, the whole brood would be at serious risk. By contrast, in a plentiful year the whole brood may fledge. However, in their review of experimental studies Amundsen and Stokland (1988) found that parents of experimentally synchronous broods raised just as many fledglings as parents of normally asynchronous broods, whether selective chick loss was mediated by sibling aggression or simple begging competition. Some studies may have been carried out in years of abundant food, but others surely occurred in poor years, when Lack's hypothesis would predict higher mortality in synchronous broods. A later review of 30 experimental studies, involving 10 passerine species and 15

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non-passerines, showed that parents of experimentally synchronous broods tended to raise more fledglings than control parents, although experimental fledglings were usually lighter, raising doubts about their subsequent survival (Amundsen and Slagsvold 1991).

Mock and Ploger (1987) showed that the apparently normal fledging success of experimentally synchronous broods of cattle egrets may be associated with hidden costs. Intense competition between same-aged nestmates for food and survival involves an extra energetic cost to parents, who bring more food to the brood (see also Fujioka 1985). Hence, synchrony could lead to diminished parental survival or fecundity in later seasons (Mock and Forbes 1994).

Mock and Ploger's (1987) interpretation rests partly on the sibling rivalry reduction hypothesis of Hahn (1981, following Hamilton 1964), which holds that age-based asymmetries reduce competition for food among broodmates by effectively dictating precedence. The practical consequence is diminished fighting, begging, and wastage of the brood's energy on sibling conflict. However, Hahn proposed that sibling conflict prejudices the current brood, whereas Mock and Ploger (1987) proposed that future broods might be prejudiced if parents absorb the cost by working harder.

The present study contrasted the brood reduction and sibling rivalry hypotheses by testing whether asynchrony in the blue-footed booby (*Sula nebouxii*) facilitates early selective chick loss (following Lack) or reduces the energetic cost of sibling conflict (following Hahn). It also examined whether the energetic cost of rivalry between synchronous nestmates is borne by parents (as suggested by Mock and Ploger). In most of its ambit the hypothesis of Hahn (1981) is complementary to that of Lack (1954) (although the two are conceptually distinct), and the two hypotheses generate some identical predictions (see Table 3 in Hahn 1981). Therefore, to contrast them we derived suites of predictions for fledging success, mortality, growth, aggression and feeding in the study species.

We chose to test Lack's and Hahn's hypotheses because they seem particularly appropriate for species whose chicks compete violently and sometimes kill each other, and because facultative brood reduction is the most widely accepted explanation. Other hypotheses for staggered hatching (review in Lessells and Avery 1989) are not considered because our data are not appropriate for testing them.

The blue-footed booby on Isla Isabel, Nayarit, Mexico has a modal clutch of two similar-sized eggs that hatch 4 days apart (Drummond et al. 1986). Often both chicks fledge, but if food is insufficient during the nestling period, the senior chick increases its aggression and the junior chick dies of starvation or expulsion from the nest (Drummond and García Chavelas 1989). In most broods there is a stable dominance relationship, with the junior chick readily submitting to its sibling and parents apparently declining to interfere in offspring agonism (Drummond et al. 1991; Drummond and Osorno 1992).

The predictions are listed in Table 1. Those related to fledging success are the most important and follow Hahn (1981); the other predictions are explicit or, in our opinion, implicit in Lack's and Hahn's original proposals. We tested the predictions by swapping chicks between nests to create synchronous broods, which were compared with broods with normal hatch intervals. This was done in 1986, when a mild El Niño

Table 1 Predictions for asynchronous (control) broods, in comparison with experimentally synchronous broods

	Brood reduction hypothesis (Lack 1954)[a]	Sibling rivalry reduction hypothesis (Hahn 1981)
Fledgling success	1. Lower proportion of broods in which both chicks die	Likewise
	2. Higher proportion of broods with partial success, relative to broods where both die	Likewise
	3. No difference in proportion of broods in which both chicks survive	Greater proportion broods in which both chicks survive
Age of victim at death	4. Younger	–
Growth	5. Greater difference between dominant and subordinate chicks	–
	6. Greater growth of senior chicks	Greater growth of both chicks
Aggression	7. Hierarchy forms (not necessarily, in synchronous broods)	Lower frequency of aggression
Feeding frequenccy	8. Greater difference between the two chicks	–

[a]Predictions for conditions of food shortage

oceanographic event depressed fish stocks in the eastern Pacific Ocean (Diaz and Kiladis 1992; Anderson 1989), presumably reducing the availability of sardines and anchovies, which are the blue-footed booby's exclusive prey. Lack's hypothesis predicts that in such a lean year asynchronous broods will outperform synchronous broods, by jettisoning the junior chick early on and fledging more senior chicks.

We also simultaneously tested the complementary hypothesis of optimal hatch asynchrony of Mock and Ploger (1987), according to which the magnitude of hatching asynchrony is adjusted to maximize parental efficiency and lifetime fitness. An experimentally enlarged hatching interval prejudiced the reproductive success of cattle egrets (*Bubulcus ibis*, Mock and Ploger 1987) and shags (*Phalacrocorax aristotelis*, Amundsen and Stokland 1988), resulting in slower growth and more frequent and early death of junior chicks, due to severe competitive disadvantage. Hence, there is an upper limit to beneficial delay in hatching between broodmates. Mock and Ploger (1987) concluded that the natural hatching interval steered an optimal course between large intervals, involving excessive competitive disparity and high mortality of junior chicks, and small intervals, involving extra foraging effort and probable diminished success of parents in subsequent reproduction.

To test the optimality hypothesis, we experimentally doubled hatching intervals in a sample of blue-footed booby broods. Compared with controls, junior chicks in broods with enlarged intervals were predicted to feed infrequently, grow poorly and die frequently.

Our analyses scrupulously took into account the differences in age between chicks in different treatments, a potential confound when feeding or aggression vary with age.

Materials and methods

Methods

The study was carried out in the blue-footed booby colony in the Costa Fragatas area of Isla Isabel between February and July 1986. Hatchlings 0–1 day old were exchanged between two-chick broods shortly after completion of hatching of the focal broods, to establish three treatments differing only in hatching interval. In synchronous broods, on the day the first egg hatched, we removed the second egg and replaced it with a 0–1 day old chick. In controls, we removed either the first ($n = 5$) or the second ($n = 7$) chick on the day it hatched and replaced it with a 0–1 day old chick. In three doubly asynchronous broods, we removed the first laid egg 4 days before its expected hatching date and replaced it with a 0–1 day old chick; in ten doubly asynchronous broods, after hatching of the first chick we temporarily replaced the second egg with another egg, then replaced the temporary egg with a 0–1 day old chick 8 days after hatching of the first chick. Mean hatching intervals were 0.16 days (SD = 0.36 days, range = 0–1 day, $n = 19$) in synchronous broods, 7.53 days (SD = 1.29 days, range = 6–9 days, $n = 17$) in doubly asynchronous broods, and 4.08 days (SD = 0.64 days, range = 3–5 days, $n = 13$) in control broods. The exchange of a chick in control broods controlled for possible effects of exchanging, for example effects associated with individual recognition. Ages of all chicks were known from daily inspection of all clutches at Costa Fragatas. When first found a chick was considered to be 0 days old.

In a fourth treatment, natural controls, two chicks were retained in their natal nest and left untouched except for the routine weighing, measuring and marking that were applied to all treatment groups; their mean hatching interval was 3.85 d (SD = 0.53 days, range = 3–5 days, $n = 14$).

As broods became available, over an 89-day period (18 February–18 May), they were assigned successively to one of the four treatments, within the limits imposed by compatibility of chicks' particular ages. Mean starting dates (± SE, days) for the four treatments were similar: 12 March (± 7.4) in synchronous broods, 6 March (± 6.3) in doubly asynchronous broods, 8 March (± 6.5) in control broods, and 16 March (± 7.3) in natural control broods. No more than one chick was swapped into a brood, with the exception of eight doubly asynchronous and control broods where the younger (resident) chick failed to hatch and was substituted by a hatchling from another nest to complete the brood. In synchronous broods there was no evidence of a relationship between origin of chick (resident or introduced) and dominance (see criterion below): 57% of introduced chicks became dominant ($G = 0.54$, $df = 1$, $P > 0.7$, $n = 14$ broods that suffered no predation). Furthermore, across all treatments, origin of chick (resident or introduced) was not related to survival: for seniors/dominants, 2 of 16 residents and 2 of 23 introduced chicks died ($G = 0.13$, $df = 1$, $P > 0.05$); for juniors/subordinates, 13 of 25 residents and 7 of 14 introduced chicks died ($G = 0.01$, $df = 1$, $P > 0.05$). However, there is limited evidence that resident chicks tended to grow faster than introduced chicks: at age 10 days, residents were 22% heavier ($F = 3.7$, $df = 1{,}48$, $P = 0.06$; three-way ANOVA, treatment × status × origin, all interactions ns), but by age 20 days no difference was evident ($F = 2.1$, $df = 1{,}30$, $P = 0.16$).

Chicks were marked with colored wire bands around the tarsus until they could walk, when numbered plastic bands were used. Until chicks reached 1000 g they were measured (culmen, with a tape measure) and weighed on an Ohaus electronic balance (± 1 g) each day between 0700 and 1000 hours. Thereafter, these measurements and masses [with a Pesola spring balance (± 25 g)] were taken every 2nd day until chicks became fully feathered (i.e., head turned completely black) at about 12 weeks of age.

We observed behaviour in 9 synchronous broods, 7 doubly asynchronous broods, 10 control broods and 4 natural control broods. Each brood was observed continuously between 0600 h and 1800 h on an average 9.6 consecutive days (SD = 3.05 d, $n = 30$) during the first 20 d after the two chicks began cohabiting. Mean ages of junior/subordinate chicks on the first day of observation were similar in the four treatments: synchronous broods, 5.7 d; doubly asynchronous broods, 5.2 d; control broods, 6.6 d; natural control broods, 3.8 d. This observation schedule was possible because hatching in the colony was staggered in time and there were four observers. Two observers alternating in two-hour shifts during 12 h watched up to four broods simultaneously. We recorded all aggressive pecks and parental feeds, following the strict behavioural definitions used in Drummond et al. (1986, 1991). Inter-observer reliability was checked at the start of the study and then once a month, by recording a total 42 nest-hours of independent observations by two observers.

Terminology and Analysis

In doubly asynchronous, control and natural control broods each chick is referred to as senior or junior, according to the age difference. In synchronous broods, each chick is referred to as dominant or subordinate, according to which nestmate gave more pecks. A chick was dominant overall if it dominated on more days than its nestmate. In the five synchronous broods that were never observed and in the one synchronous brood in which the two nestmates were dominant on equal numbers of days, we attributed dominance to the chick that was heavier than its nestmate on the majority of days up to age 40 days (beyond 40 days sexual size dimorphism is increasingly likely to reverse differences in size due to dominance). Differences of age or dominance are both referred to as status.

Following Drummond et al. (1991), disappearances of chicks up to 6 days old were attributed to predation by milk snakes (*Lampropeltis triangulum*). Despite differences among treatments in the initial ages of chicks, the proportions of broods that suffered predation did not differ ($G = 0.72$, $df = 3$, $P > 0.8$; doubly asynchronous: 4/17, synchronous: 5/19, control: 1/13, natural control: 4/14).

Growth was analyzed by comparing mean weights and lengths of culmen and ulna at hatching (0 days), 10 days and 20 days (ages when brood reduction is common), and 60 days (the greatest age for which the diminishing sample sizes were adequate). Only chicks with surviving nestmates at the time of measuring were used. Sex was taken into account in comparisons of 60-days old chicks (using three-way ANOVAs), but not in the case of younger chicks (for which two-way ANOVAs were used) because the sex of many younger chicks was unknown. Directional hypotheses requiring a pairwise contrast were tested with *t*-tests. Sex of fledglings was identified using a discriminant function based on asymptotic lengths of culmen and ulna of fledglings in 1987 (Drummond et al. 1991). To determine whether chicks were underweight at death we compared their last weight (the day before death) with the mean weight of their peers (chicks of the same treatment, status and age).

If a chick died, then its brood was deleted from behavioral analyses from that date onward. To achieve meaningful comparisons of behavioral frequencies despite necessary disparities between treatment groups in ages of chicks, data were grouped either by date or by age. Analyses by date used the scores of both nestmates recorded on the same day, and the scores were associated with the age of the senior chick on that day. Analyses by age used the scores of both nestmates at a particular age, for example the score of the senior chick on its 5th day of life and the score of the junior chick on its 5th day of life. To compare treatments for total feeding frequency to the brood (summing across both parents and both chicks), a mean frequency was calculated for each brood over a 10-day block by date, and a 10-day block by age. To compare allocation of feeds between nestmates, feeding scores of both chicks of the same age were used and a mean was calculated for each brood over a 10-day block. To compare treatments for total pecking frequency (summing the two nestmates), we added the scores of the two chicks at the same age, then calculated a mean for each brood for a 10-day block. We also compared the pecking frequencies of senior chicks in control broods and dominant chicks in synchronous broods using similar 10-day blocks by age. Doubly asynchronous broods posed an even greater problem for establishing meaningful comparisons of chicks at equivalent ages. We compared total pecking frequency in doubly asynchronous and control broods by grouping scores according to the age of the junior nestmate, and also compared pecking frequencies of senior chicks in these two treatments at age 11–20 days. Apparent inconsistencies in sample sizes in Results arise from using these different methods of grouping data.

For analyses of fledging success and mortality we used the G test with Williams correction (Sokal and Rohlf 1981), except when there was a zero value, in which case we used Fisher's exact test. Except where stated otherwise, significance tests were one-tailed tests of directional hypotheses. Pairwise comparisons were made with the Mann-Whitney *U*-test.

Results

Control versus natural control

There were some differences in growth between control broods and natural control broods, the latter tending to grow more slowly. We therefore discarded the data from the natural controls and compared the two experimental treatments only with the controls, which represented a more strictly appropriate comparison.

Control and natural control treatments did not differ in the proportion of broods that produced 0, 1 or 2 fledglings, whether predated broods were included ($G = 0.71$, $df = 2$, $P > 0.3$) or deleted ($G = 1.55$, $P > 0.2$). Nor did they differ in behavioural frequencies up to age 20 days (pecks, 0–10 days: $U = 5$, $P > 0.4$, $n = 3, 6$; pecks, 11–20 days: $U = 12$, $P = 1.0$, $n = 4, 6$; feeds, 0–10 days: $U = 6.5$, $P > 0.7$, $n = 3, 6$; feeds, 11–20 days: $U = 10$, $P > 0.7$, $n = 4, 6$; all two-tailed tests).

However, two-way analyses of variance (treatment × status) revealed significant differences between control and natural control broods, in the weight of broods (senior plus junior chicks) at ages 10 days and 20 days. Control broods were heavier than natural controls at 10 d ($F = 5.43$, $P = 0.025$, $df = 1, 38$) and at 20 days ($F = 6.05$, $P < 0.02$, $df = 1, 32$), averaging 18% and 21% heavier at those respective ages. Although these differences diminished progressively with age, they prevent us pooling the two treatments for comparing with experimental treatments. By contrast, hatchlings of the three main treatment groups were similar in weight, culmen length and ulna length ($P > 0.4$, all three ANOVAs).

The differences between controls and natural controls may be partly explained by a fortuitous difference in sizes of chicks at hatching: at 0 days, senior and junior control chicks had culmens 5% and 1% longer, respectively, than their natural control peers.

Brood reduction and sibling rivalry reduction

Here we report the results relevant to the predictions from Lack's and Hahn's hypotheses presented in Table 1; we refer to the predictions according to the numbering in that table.

Fledging success and mortality

Similar proportions of synchronous broods and control broods fledged 0, 1 or 2 chicks (Table 2), and it was mainly subordinate and junior chicks that died, with indications that they were victims of sibling aggression and starvation. In synchronous broods, five of six single losses were the subordinate chick, and four of the five were underweight ($\bar{x} = 28\%$ below peer mean). One day before death, one of these subordinate victims was found 5 m from its nest bearing wounds from adult pecks, evidently a victim of expulsion and consequent persecution by neighbors. In control broods, all seven losses were chicks that were underweight ($\bar{x} = 42\%$). Four of these victims were junior

Table 2 Number (and proportion) of broods fledgling 0, 1, 2 chicks in relation to hatching interval

Treatment	n^a	Number of fledglings 0	 1	 2
Synchronous	14	0 (0.00)	6 (0.43)	8 (0.57)
Doubly asynchronous	13	1 (0.07)	9 (0.69)	3 (0.23)
Control	12	1 (0.08)	5 (0.42)	6 (0.50)

[a] Including only unpredated broods

chicks, three of which were subject to intense pecking in the days before death.

The first two predictions of Lack's and Hahn's hypotheses were not supported (Table 2). When all broods (including predated broods) were analyzed, the proportion of broods suffering total loss was not lower in control broods than in synchronous broods ($G = 1.78$, $df = 1$, $P > 0.10$); and the ratio of broods with one fledgling to broods with no fledglings was no higher in control broods than in synchronous broods ($G = 1.83$, $df = 1$, $P > 0.10$). Moreover, when predated broods were deleted from the sample, neither of these same comparisons was significant ($P > 0.50$ and $P > 0.46$, respectively, Fisher's test; Table 2). Contrary to Hahn's prediction (no. 3) the proportion of broods in which both chicks survived was not higher in control broods than in synchronous broods, whether all broods were included in the comparison ($G = 0.06$, $df = 1$, $P > 0.70$) or only unpredated broods ($G = 0.11$, $df = 1$, $P > 0.70$; Table 2).

Samples of broods were small and consequently inadequate to detect minor differences in mortality between control and synchronous broods, but it is noteworthy that no tendencies in the predicted directions were evident (Table 2).

The data provide nonsignificant support for Lack's fourth prediction: junior chicks in control broods died at a younger mean (± SD) age (14.9 ± 9.94 days) than subordinates in synchronous broods (23.5 ± 29.17 days) (Mann-Whitney $U = 12.5$, $P = 0.5$, $n = 5,5$).

Growth

Overall, the predictions of both hypotheses in relation to growth were not supported by significant results or tendencies in the data. Contrary to prediction 5 of Lack's hypothesis, there was little indication that the growth of nestmates differed more in control broods than in synchronous broods. Compared with synchronous broods, the difference in weight between control nestmates was 17% greater at 10 days, 60% less at 20 days and 42% less at 60 days (Fig. 1), but none of these contrasts was significant (10 days: $t = 0.26$, $P = 0.80$, $n = 11, 11$; 20 days: $t = 0.57$, $P = 0.57$, $n = 9, 8$; 60 days: $F = 0.43$, $P = 0.67$, $n = 5, 7$). And similar patterns of nonsignificant contrasts between synchronous and control broods were found for differences between nestmates in length of culmen and length of ulna (Osorno 1991).

Contrary to prediction 6 of Lack's hypothesis, senior chicks in control broods did not grow faster than dominant chicks in synchronous broods. Compared with dominants in synchronous broods, seniors in control broods were 2.4% heavier at 10 days, 7.3% lighter at 20 days and 7.0% lighter at 60 days (Fig. 1), but none of these contrasts was significant (10 days: $t = 0.24$, $P = 0.81$, $n = 12, 11$; 20 days: $t = 0.82$, $P = 0.42$, $n = 10, 8$; 60 days: $F = 2.52$, $P = 0.15$, $df = 1, 8$).

Contrary to Hahn's hypothesis (prediction 6), asynchronous chicks did not grow better than synchronous chicks; if anything, there was a nonsignificant tendency in the contrary direction. Compared with synchronous broods, controls were 1.2% lighter at 10 days, 1.2% heavier at 20 days and 0.2% lighter at 60 days, and none of these contrasts was significant (10 days: $F = 0.01$, $P = 0.86$, $df = 1, 41$; 20 days: $F = 0.18$, $P = 0.67$, $df = 1, 31$; 60 days: $F = 0.01$, $P = 0.92$, $df = 1, 20$). Similar patterns of nonsignificant contrasts were found for culmen and ulna (Osorno 1991).

We used a multivariate test to simultaneously examine the possible effects of treatment, status, and sex on both the maximum weight and age at which that weight was reached. Neither the maximum weight nor the age at which it was reached differed between synchronous and control broods (treatment: $F = 0.52$, $P > 0.05$, $df = 2, 20$; status: $F = 0.28$, $P > 0.05$, $df = 2, 20$). Females in both treatments reached a greater weight than males and did so later than males (sex: $F = 39.37$, $P < 0.001$, $df = 2, 20$). There was no interaction between status and maximum weight or age of maximum weight ($F = 1.24$, $P > 0.05$, $df = 2, 20$). (Similar intrasexual differences in maximum weight and the age it is attained were reported by Drummond et al. 1991.)

Aggression and feeding

We observed aggression in nine of ten control broods; in the brood without aggression the junior chick steadily lost weight and died 2 days after the brood was formed. In the nine control broods with aggression, it was the senior chick that dominated, consistently in most cases (days of dominance of senior/junior, per brood: 10/0, 10/0, 9/1, 8/0, 7/0, 7/1, 6/0, 5/0, 3/2). Pecking started when the senior chick was 6.8 ± 0.57 days old ($n = 3$), at which time it enjoyed an obvious advantage in motor coordination and was larger than its nestmate (weight: 36–52%, culmen: 16–23%, ulna: 7–20%).

In most of the nine synchronous broods there was also consistent dominance by one chick, contrary to

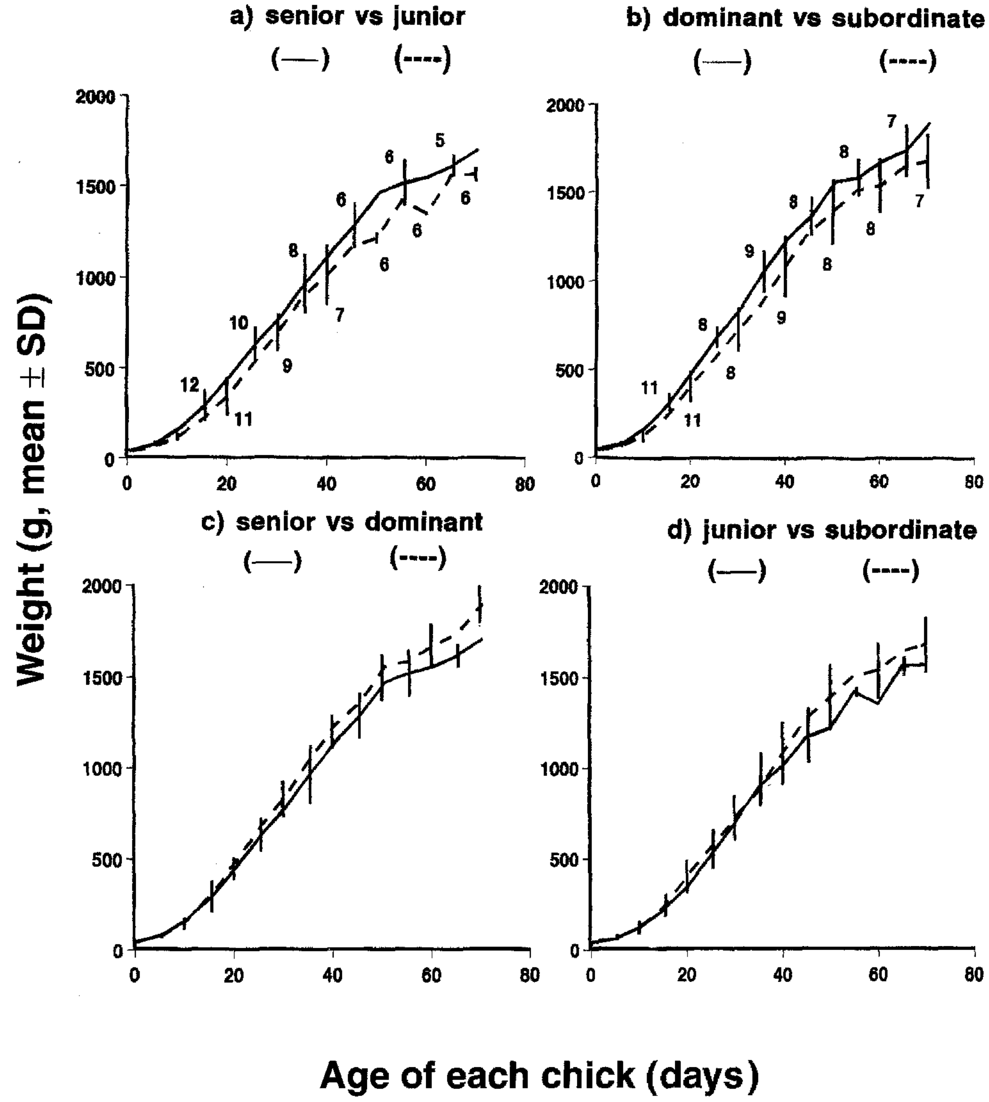

Fig. 1a–d Growth of synchronous and control broods. Synchronous broods included one dominant and one subordinate chick, control broods included one senior and one junior chick. Graph **a** compares nestmates in control broods, **b** compares nestmates in synchronous broods; the same data are presented in graphs **c** and **d** to compare chicks of the same status in synchronous versus control broods. All graphs compare chicks of the same age. Numbers by curves are sample sizes

Lack's hypothesis (prediction 7); days of dominance by dominant/subordinate, per brood: 17/1, 11/0, 10/0, 6/3, 4/3, 4/0, 4/0, 2/0, 1/1. Pecking in synchronous broods started when the chicks were 6.8 ± 0.71 days old ($\bar{x}$ ± SE, $n = 6$). In three of six broods where the start of pecking was observed, the dominant chick was initially larger than its nestmate (weight: 26.8 ± 2.3%, culmen: 14.5 ± 1.3%, ulna: 8.9 ± 3.1%); but in the other three broods the dominant chick was initially slightly smaller than its nestmate (weight: − 4.9 ± 2.1%, culmen: − 0.2 ± 4.3%, ulna: − 3.3 ± 0.2%). Two of these three smaller dominants became larger than their nestmates, and the nestmate of the third one died on the day after aggression started. In seven of nine synchronous broods observed the dominant chick was also the heavier nestmate until at least 40 days or until one chick died. The two exceptions were a brood where both chicks grew poorly and the subordinate died after 6 days of cohabitation, and a brood in which the chick that was consistently lighter (by no more than 200 g) dominated on 17 of 18 days.

Consistent with Hahn's prediction (no. 7), pecking by the two nestmates was 60% more frequent in synchronous broods than in control broods at age 11–20 days (analysed by age), but the difference fell just short of significance ($U = 6.5$, $P = 0.06$, $n = 5, 6$; Fig. 2). However, at this age dominant chicks in synchronous broods pecked their nestmates 3 times more frequently than senior chicks in control broods (61.0 ± 18.1 and 20.9 ± 7.1 pecks, respectively), and this difference was significant ($U = 6.0$, $P = 0.03$, $n = 6, 6$). At 0–10 days, when chicks were first acquiring the ability to peck, these frequencies were low and similar in synchronous and control broods ($U = 19$, $P > 0.47$, $n = 5, 8$; Fig. 2).

Consistent with Lack's prediction (no. 8), the difference in the feeding frequencies of two nestmates across the whole 0–20 day span was 2.6 times greater in control broods than in synchronous broods ($U = 16.5$, $P = 0.05$, $n = 7, 9$), when analysed by age (Fig. 3). This difference was significant at 11–20 days ($U = 3$, $P = 0.03$, $n = 4, 6$) and non-significant at 0–10 days ($U = 13$, $P = 0.18$, $n = 5, 8$).

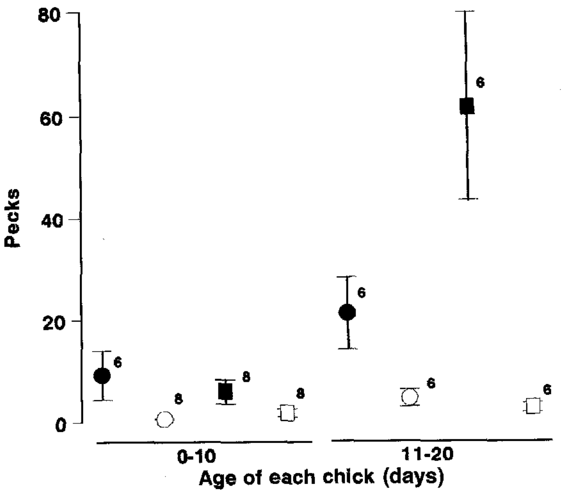

Fig. 2 Aggression in synchronous and control broods. Pecks (mean ± SE) by dominants ■ and subordinates □ in synchronous broods, and seniors ● and juniors O in control broods. *Numbers by bars* are sample sizes

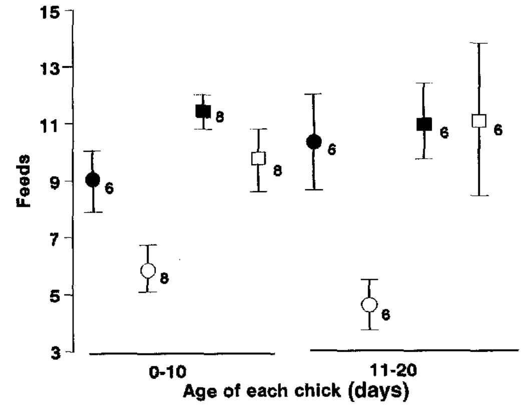

Fig. 3 Feeding in synchronous and control broods. Daily frequency of feeds (mean ± SE) by dominants ■ and subordinates □ in synchronous broods, and seniors ● and juniors O in control broods. *Numbers by bars* are sample sizes

Importantly, synchronous broods were fed more frequently than control broods, when frequencies of feeds by both parents to both nestlings were analysed by age. At 0–10 days, synchronous broods consumed 30% more feeds than controls (21.1 ± 1.4 and 14.0 ± 1.7 feeds respectively; $U = 2.5$, $P < 0.003$, $n = 6, 8$; Fig. 3); at 11–20 days, synchronous broods consumed 21% more feeds than controls, though this latter difference was not significant (22.3 ± 3.4 and 16.8 ± 2.4 feeds respectively; $U = 7.5$, $P > 0.12$, $n = 5,6$; Fig. 3). Most of the difference between sample means of the treatments was evidently due to juniors feeding less frequently than seniors in control broods whereas subordinates fed at a similar rate to dominants in synchronous broods (Fig. 3).

Optimal hatch asynchrony

Fledging success and mortality

Three-quarters of junior chicks in doubly asynchronous broods died. Although this was 50% more than in control broods (Table 2), the difference was not significant, whether predated broods were excluded ($G = 1.87$, $df = 1$, $P < 0.2$) or included ($G = 3.38$, $df = 1, P < 0.1$). Doubly asynchronous juniors and control juniors died at similar ages (13.1 ± 7.9 days and 14.9 ± 8.9 days, respectively; $U = 22$, $P > 0.05$, $n = 5, 10$).

Seven of ten juniors that died in doubly asynchronous broods were underweight ($\bar{x} = 28 \pm 15.9\%$, $n = 7$) before death, and seven corpses were found, four in the nest and three outside it. Taken with the observations of aggression (below), these data imply that most died from expulsion or aggressively imposed starvation.

Growth

As predicted, junior chicks grew more slowly in doubly asynchronous broods than in control broods: at 10 days they were 11% lighter than controls ($t = 0.99$, $P > 0.05$, $df = 18$), by 20 days they were 43% lighter ($t = 2.77$, $P < 0.02$, $df = 11$), and the difference appeared to persist thereafter but was not significant (Table 3). A similar pattern of significant and nonsignificant differences between juniors in the two treatments was found for length of culmen and ulna (Osorno 1991).

Senior chicks in both treatments grew very similarly (weight at 10 days: $t = 1.17$, $P = 0.26$, $df = 23$; 20 days: $t = 0.07$, $P = 0.95$, $df = 16$; Table 3).

Table 3 Growth (mean ± SD) in doubly asynchronous (*DA*) and control (*C*) broods

	Senior chicks				Junior chicks			
	n		weight (g)		*n*		weight (g)	
Age (days)	DA	C	DA	C	DA	C	DA	C
0	12	12	44 ± 3	44 ± 9	12	11	42 ± 4	41 ± 5
10	13	10	153 ± 32	171 ± 41	9	9	120 ± 40	135 ± 21
20	8	8	458 ± 95	455 ± 101	4	7	252 ± 99	440 ± 105*
60	3	3	1508 ± 122	1560 ± 78	3	4	1313 ± 107	1547 ± 220

* Significantly different at 0.05 level (*t*-test). Other differences between treatments, at 10 days and 60 days, were not significant

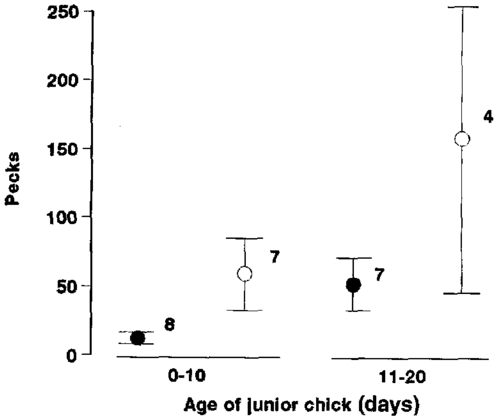

Fig. 4 Aggression in doubly asynchronous and control broods. Daily frequency of pecks (mean ± SE) by both nestmates (summed) in doubly asynchronous O and control broods ●. *Numbers by bars are sample sizes*

Aggression and feeding

Doubly asynchronous broods were significantly more aggressive than controls; the two chicks gave nearly 5 times as many pecks when the junior chick was 0–10 days old ($U = 8$, $P = 0.01$, $n = 7, 8$) and nearly 3 times as many pecks when the junior chick was 11–20 days old (Fig. 4), although the latter difference was not significant ($U = 13$, $P > 0.05$, $n = 4, 6$). Because of sample size limitations, we could compare pecking of seniors only at age 11–20 days, when the doubly asynchronous seniors pecked more than 3 times as frequently as control seniors (70.3 ± 38.8 and 20.9 ± 7.0 pecks, respectively), although the difference fell short of significance ($U = 10$, $P = 0.07$, $n = 6, 7$).

Feeding rates to juniors in doubly asynchronous broods and control broods were similar at 0–10 days (5.8 ± 0.6 and 6.0 ± 0.8 feeds respectively; $U = 25$, $P = 0.39$, $n = 8, 7$), and at 11–20 days (5.1 ± 1.6 and 4.6 ± 0.8 feeds respectively; $U = 11$, $P = 0.46$, $n = 6, 4$).

Discussion

We assume our observations were made under conditions of food shortage, since there was an ongoing El Niño event during the study, roughly half of all broods observed suffered starvation mortality, and the overall reproductive success of the colony was relatively poor in 1986 (H. Drummond, unpublished work).

The patterns of mortality and growth predicted by the brood reduction hypothesis of Lack (1954) for conditions of food shortage and by the sibling rivalry reduction hypothesis of Hahn (1981) were not demonstrated. In view of our small samples and consequent low statistical power, the negative results reported here are not conclusive, but it is noteworthy that the predicted patterns of mortality and growth were not even suggested by tendencies in the data. With or without a 4-day hatch interval, nestmates established a relationship of aggressive dominance, and this apparently led to starvation-related mortality of the subordinate chick in about half of the broods studied. Experimentally synchronous broods were more aggressive than asynchronous controls, but there was no evidence that increased aggression led to poorer growth or greater mortality of chicks.

Hence, *contra* Lack, a hierarchy formed even without a hatching interval (cf. Skutch 1976, Bancroft 1985), and *contra* Hahn (1981), hierarchy formation in the absence of an age difference evidently did not involve costs in terms of growth or survival of offspring. Nonetheless, experimental synchrony evidently did impose a cost on parents, if we assume that elevated feeding frequencies to synchronous broods reflect greater parental effort. Since more frequent feeding of synchronous broods did not lead to faster growth, it is likely that the extra food was used to fuel increased conflict between nestmates. Parents may have increased their foraging effort to compensate for energy lost through sibling conflict. In other words, parents of synchronous broods may have masked the effects expected under Hahn's hypothesis by compensating for elevated energy consumption of chicks.

There is support in these data for a modified version of Lack's hypothesis that asynchrony functions to facilitate brood reduction. Even without asynchrony, one chick became aggressively dominant and apparently was able to ensure that the effects of food shortage fell mainly on its sibling, resulting in poor growth and in some cases death. In the blue-footed booby asynchrony is not required for the occurrence of social dominance, feeding priority and brood reduction (*sensu* Mock, in press). However, subordinate chicks in asynchronous broods received inferior shares of parental food and may have died earlier than in synchronous broods, which suggests that asynchrony leads to more prompt and efficient brood reduction, as envisaged by Lack and demonstrated in experimental studies of other species (Slagsvold 1982; Haydock and Ligon 1986; Gibbons 1987). According to this interpretation, in some avian species asynchrony facilitates brood reduction, but the reduction would occur anyway, even without staggered hatching.

The proposal of Hahn (1981) that asynchrony lowers the intensity and cost of conflict between nestmates is probably right. However, it seems that the extra cost of conflict between synchronous chicks is borne not by the chicks but by parents, whose lifetime fitness is likely to be prejudiced by increased foraging, as suggested by Mock and Ploger (1987) for cattle egrets. Paradoxically, the extra cost of conflict in synchronous broods seemed to involve greater aggression by the dominant chick and greater feeding by the subordinate chick, in comparison with asynchronous broods. Possibly subordinate chicks engaged heavily in costly activities that we did not record, such as begging and evading aggression.

Exaggerated asynchrony probably leads to diminished parental reproductive success. Junior chicks grew poorly and suffered abnormally high rates of aggression, probably leading to increased mortality (although the observed increase was not significant). The possible adaptive significance of elevated pecking by senior chicks in doubly asynchronous broods is puzzling, but the phenomenon seems real: in natural broods comprising highly asymmetric chicks derived from the first and third eggs in a clutch, intense aggression by the elder chick is common (personal observation).

Our results show that of the three hatching intervals tested, normal asynchrony probably serves parental interests best, at least under the prevailing ecological conditions at the study site. In comparison, synchronous broods produce similar numbers of fledglings but at greater cost, and exaggeratedly asynchronous broods probably produce fewer fledglings because junior chicks are attacked frequently and grow poorly.

Overall, the evidence suggests that one function of hatching asynchrony in the blue-footed booby is reduction of sibling rivalry, which might otherwise prejudice future survival or fecundity of parents. In addition, asynchrony may facilitate early death of junior chicks, although there is as yet no evidence that this benefits parents. In avian species without violent sibling conflict asynchrony may have different effects, and in blue tits (*Parus caeruleus*) there is evidence that it affects relative survival of male and female parents through effects on the division of brood care (Slagsvold et al. 1994).

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