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Author(s): D. J. Anderson
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The role of hatching asynchrony in siblicidal brood reduction of two booby species

D.J. Anderson*

Department of Biology, Leidy Laboratory, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

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Summary. Hatching asynchrony (HA) of masked boobies (*Sula dactylatra*) in the Galápagos Islands differs from that of its sympatric congener, the blue-footed booby (*S. nebouxii*), in association with differences in brood reduction systems. Masked booby nestlings are obligately siblicidal, have long HA, and the probability and timing of siblicide is strongly influenced by HA. Blue-footed boobies are facultatively siblicidal and have shorter HA. Experimental shortening of masked booby HA demonstrated that this species maintains its HA above an "early reduction threshold", below which parents may incur costs of provisioning a brood that they cannot raise to fledging, but that blue-footed booby HA occur above, at, and below the masked booby threshold. Differences in HA alone cannot explain the differences between these two brood reduction systems.

Introduction

Asynchronous hatching within avian broods can affect subsequent interactions among nest mates. Chicks at the beginning of the hatching sequence have a developmental advantage over later-hatched chicks that may confer a competitive advantage for access to limited parental care. This advantage is most apparent in large predatory species, in which lethal sibling aggression (siblicide) causes substantial nestling mortality (Stinson 1979; Braun and Hunt 1983; Fujioka 1985a, 1985b; Mock 1984a, 1984b, 1985; Cash and Evans 1986; Drummond et al. 1986; Mock and Ploger 1987). Of the several extant adaptive (Lack 1954; Hussell 1972, 1985; Clark and Wilson 1981; Hahn 1981; Magrath 1988) and non-adaptive (Mead and Morton 1985) hypotheses concerning the evolution of hatching asynchrony (HA), field studies of siblicidal birds support the "brood reduction" (Lack 1954; Ricklefs 1965) and the "sibling rivalry reduction" (Hamilton 1964; Hahn 1981) hypotheses (Hahn 1981; Fujioka 1985b; Mock and Ploger 1987, refs. in Mock et al. 1987).

These two hypotheses both state that parents use HA to establish a competitive hierarchy among nestlings, and that selection adjusts HA to maximize parental fitness. Species-specific HAs are thus expected to produce patterns of nestling mortality that maximize parental fitness. Experimental adjustments of HA have demonstrated its influence on competitive relationships in siblicidal species (Parsons 1975; Hahn 1981; Fujioka 1985b; Hébert and Barclay 1986; Mock and Ploger 1987), and Hahn (1981) and Mock and Ploger (1987) found that natural HAs produced higher estimates of parental fitness than did experimental HAs. However, other studies have found the opposite result, or no difference at all (Fujioka 1985b; Hébert and Barclay 1986); Stokland and Amundsen (1988) review literature on experiments with non-siblicidal species. This disagreement over the issue of whether, and to what end, selection adjusts HA in siblicidal birds may reflect the experimental approach used in the above studies: short-term treatments and short-term responses were thought to indicate lifetime reproductive success in these long-lived, iteroparous birds. However, the logistical problems inherent in measuring relevent long-term variables (offspring post-fledging survival and subsequent reproduction, residual parental reproductive value) make more comprehensive experimental studies difficult.

An alternative comparative approach to study the evolution of HA has strengths and weaknesses that complement those of the experimental approach. Comparative analysis can examine varia-

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* *Current address:* Department of Avian Sciences, University of California, Davis, CA 95616-0690, USA

tion across species in HA, and association with other life-history and ecological traits, but cannot assign causality to associations. One may partially overcome this difficulty by comparing species that have different HAs, but otherwise resemble each other phylogenetically and ecologically. Edwards and Collopy (1983) used this approach to show that obligately siblicidal eagles have longer HAs than do facultatively siblicidal eagles, and inferred that HA in this group was adapted to control the outcome of sibling aggression.

Here I use both comparative and experimental approaches to study the role of HA in two different brood reduction systems present in the boobies (family Sulidae). Masked boobies (*Sula dactylatra*) lay clutches of one or two eggs, and if both eggs hatch the brood size is reduced to one chick by obligate siblicide (Mock 1984a) (the first-hatching chick pushes its sibling from the nest scrape) shortly after the second chick hatches (Dorward 1962; Kepler 1969; Woodward 1972; Nelson 1978). Siblicide always occurs even when hatchlings are size-matched (Nelson 1967); Dorward (1962) suggested that a clutch of more than one egg may nonetheless be adaptive as insurance against the first offspring's death as an embryo or hatchling. Blue-footed boobies (*S. nebouxii*) lay one to three eggs, and siblicidal brood reduction is common at times (Nelson 1978; Drummond et al. 1986) but may be rare or absent (Anderson, unpublished data). Non-lethal aggression, in the context of hierarchical dominance interactions, occurs regularly in blue-footed booby broods (Nelson 1978; Drummond et al. 1986). In contrast to this difference in brood reduction system, these two congeners have ecological similarities. Both are tropical ground-nesting piscivores (Nelson 1978) and have similar diets (Anderson 1989a) although their foraging behavior differs (Anderson and Ricklefs 1987). I use field data on these two species to test two hypotheses regarding the role of HA in controlling sibling interactions and the probability of brood reduction.

1. HA has a causal effect on the outcome of sibling aggression;
2. species-specific differences in HA can explain differences between the species in the outcome of sibling aggression.

Materials and methods

I studied booby breeding biology at Punta Cevallos, Isla Española in the Galápagos Islands (see Anderson and Ricklefs 1987) during 3 breeding seasons (Jan.–March 1984, Jan.–March 1985, Jan.–May 1986). This period fell between the El Niño-Southern Oscillation events of 1982–83 and 1986–87 (see Anderson 1989a), and both masked and blue-footed boobies (approximately 3500 and 150 pairs, respectively) bred successfully in all 3 years at this site. My assistants and I recorded nest histories and measured chick growth of approximately 250 masked booby and 50 blue-footed booby breeding attempts in each season. We checked nests daily between 12.00 and 14.30 h, marking newly laid eggs, weighing chicks with 100 g Pesola spring scales, and measuring manus legth. When two chicks were present in a nest, we identified them by plumage development and relative body sizes; I confirmed the reliability of this technique by individually marking chicks in 8 nests with colored leg rings. In this paper I refer to first-hatching chicks as "A-chicks" and to second-hatching chicks as "B-chicks". I excluded three 3-egg blue-footed booby clutches from analyses presented here.

A chick was recorded as hatched at a given mid-day nest check when the chick was completely outside its eggshell or the chick was still attached to the eggshell but had split the eggshell into two halves. Brood reduction was recorded when a chick was absent from its nest scrape at a particular day's nest check and did not subsequently return; frequently chicks of both species returned to their nest scrape after being recorded outside the scrape as a result of their own disorientation or of sibling aggression. Thus, hatching asynchrony and time required for brood reduction were measured in increments of one day.

I estimated size disparities between nest mates on a given date with the ratio of the A-chick's weight to the B-chick's weight. In particular, I calculated the Hatching Weight Ratio on the day of the B-chick's hatching.

In 1986, I reduced HA at 10 masked booby nests containing a 1 or 2 day old nestling by replacing unhatched eggs with nestlings that had hatched on that day from other nests. I then treated these relatively synchronous twins in the same manner as unmanipulated twins until brood reduction occurred or until the A-chick reached 20 days of age. The age of 20 days is critical because at that age combined daily food intake of twins exceeded the peak intake of single chicks, which occurs at 80 days (Anderson 1989b). Similar experiments with blue-footed booby broods all failed during a period of heavy rainfall that did not affect masked boobies.

Results

Brood size reduction from 2 chicks to 1 chick occurred in 94 of 96 unmanipulated masked booby nests within 10 days of the B-chick's hatching. The B-chick, rather than the A-chick, died in all cases. Previous studies documenting the role of sibling aggression in brood reduction (Dorward 1962; Kepler 1969; Nelson 1978, p. 411) were corroborated by observations in all 3 years. Aggression occurred in 34 (40%) of 86 nest watches; attacks were directed by the A-chick to the B-chick in most (82%) cases; and actual ejection of the B-chick from the nest scrape was observed in 12 broods. Death resulted from exposure or predation outside the nest or starvation in the nest. The B-chick simply disappeared between nest checks in cases where ejection was not observed; the circumstances never contradicted the most likely interpretation that the

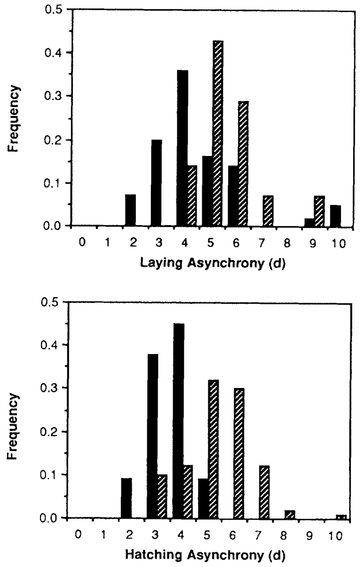

Fig. 1. Distributions of laying and hatching asynchronies in masked boobies (▨) and blue-footed boobies (■)

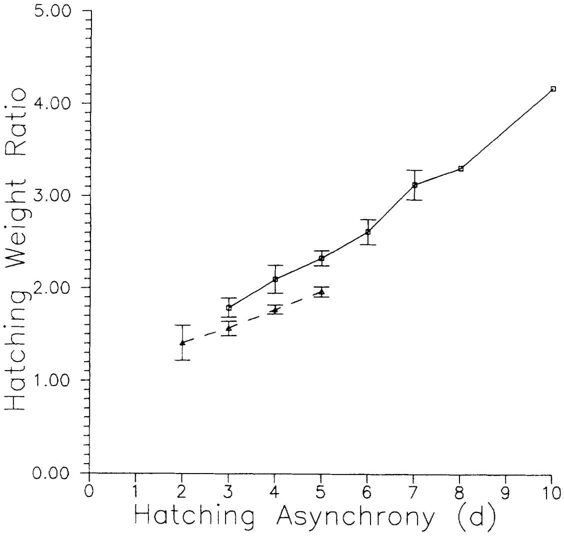

Fig. 2. Relationship between Hatching Weight Ratio and HA in masked (solid line) and blue-footed (dashed line) boobies. Lines connect means (with 1 standard error) within HA classes

Table 1. Means (SE) of breeding parameters of masked and blue-footed boobies

	Masked booby	Blue-footed booby
Laying asynchrony (d)*	5.57 (0.34)	4.48 (0.27)
Hatching asynchrony (d)**	5.36 (0.15)	3.53 (0.11)
Hatching weight ratio**	2.47 (0.07)	1.68 (0.05)
Days to brood reduction	1.76 (0.18)	–
Reduction weight ratio	2.97 (0.09)	–

* $P<0.05$; ** $P<0.001$

B-chick was ejected from the nest and then taken by a predator. I observed Galápagos mockingbirds (*Nesomimus macdonaldi*), frigatebirds (*Fregata* spp.), and marine crabs (*Grapsus grapsus*) removing ejected chicks from nest sites.

In contrast, nestling mortality from any source was rarely observed among blue-footed booby chicks of the same age, although sibling aggression occurred in 5 (26%) of 19 nest watches where A-chicks were less than 20 days old (see also Nelson 1978, p. 565). Among 42 2-egg clutches in which both eggs hatched (this total does not include cases where the A-chick died before the B-chick's hatching), one of the chicks died within 10 d of the B-chick's hatching in 7 of the nests. I observed a predator remove one of these chicks, but did not determine the cause of death of the remaining 6. Thus, incidence of siblicidal brood reduction in my sample of young blue-footed boobies lies between 0 and 0.14 (6/42). No siblicide occurred in blue-footed booby broods past the B-chick's age of 10 days in any of the 3 years. All mortality in these older chicks could be attributed to depredation by Galápagos Hawks (*Buteo galapagoensis*).

I calculated mean laying asynchrony, HA, and Hatching Weight Ratio for masked and blue-footed boobies, and mean number of days to brood reduction for natural masked booby broods during all 3 years of the study; none of these parameters were heterogeneous across years (all one-way ANOVA P-values >0.10). In comparison with blue-footed boobies, masked boobies had longer laying asynchronies (Student's $t=2.11$, $df=56$, $P=0.04$), longer HAs (Student's $t=8.67$, $df=126$, $P<0.001$), and larger Hatching Weight Ratios (Student's $t=6.01$, $df=97$, $P<0.001$) (Table 1). Although the distributions of HA overlapped, most blue-footed boobies hatched over 3–4 days, while most masked booby broods hatched over 5–6 days (Fig. 1).

Hatching Weight Ratio was highly dependent on HA in both masked ($F_{1,72}=50.88$, $P<0.001$, $r^2=0.41$) and blue-footed boobies ($F_{1,23}=14.49$, $P=0.001$, $r^2=0.39$) (Fig. 2). The relationship between these two variables, for HA values between 3 and 5 days, did not differ between the two species in terms of slope (ANCOVA, species by HA interaction $F_{1,60}=0.20$, $P=0.66$). With the interaction term omitted from the model, both HA ($F_{1,61}=17.73$, $P<0.001$) and species ($F_{1,61}=9.35$, $P=0.003$) effects were statistically significant. Thus, the significant difference in Hatching Weight Ratio (Table 1) was due both to different mean HAs of

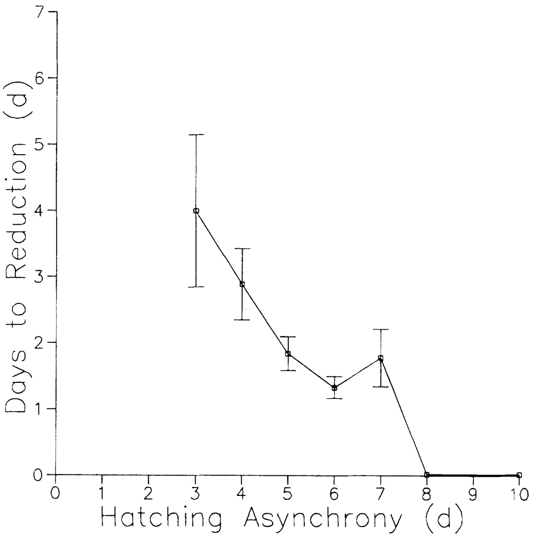

Fig. 3. Time required for brood reduction as a function of HA in masked boobies. Lines connect means bracketed by 1 S.D.

the two species and to species differences in other determinants of early post-natal body mass (possibilities include differential provisioning of eggs and species differences in early post-natal growth rate (Stockland and Amundsen 1988)).

Masked booby A-chicks ejected their younger siblings within 0–8 days of the B-chick's hatching (Table 1). The amount of time an A-chick required to reduce the brood was related to the degree of HA of the brood ($F_{1,74}=21.87$, $P<0.001$, $r^2=0.23$) (Fig. 3). The advantage that older A-chicks have in ejecting a nestmate could be due to their larger relative size, and/or enhanced motor or other abilities associated with more advanced developmental status. I separated the effects of body size on time to brood reduction from other effects associated with increasing age by regressing the number of days to brood reduction on Hatching Weight Ratio; the residuals from this regression were then regressed on HA. Both Hatching Weight Ratio ($F_{1,70}=12.26$, $P=0.001$, $r^2=0.15$) and residual effects of HA ($F_{1,70}=5.76$, $P=0.02$, $r^2=0.08$) accounted for significant variation in time to brood reduction. However, together they explained only 23% of the total variation in that parameter. Variation in factors such as incident solar radiation (B-chicks were more likely to return successfully to the scrape on cloudy than on sunny days) and foraging success of parents (influencing growth and thus size differences) may contribute to this variation also.

No clear evidence exists, within the normal range of masked booby HA, of a threshold HA below which early brood reduction is not inevitable. However, the experimental broods extended the range of HA beyond the normal lower limit of 3 days. These broods showed that HAs of less than 3 days were associated with increased persistence of the B-chick in the nest, and that the probability of brood reduction prior to B-chick day 20 was reduced, relative to HAs of 3 days or greater (Table 2). Thus, a 3 day HA approximates a threshold above which early siblicidal brood reduction is nearly certain and below which is uncertain or delayed (Table 2).

Table 2. Proportions of experimental (^{E}) and unmanipulated masked booby broods in which the B-chick was not ejected within 20 d of hatching

	Hatching asynchrony					
	1^E	2^E	3	4	5	5<
Proportion of broods not reduced within 20 d of b-chick's hatching	0.71	0.33	0.11	0.00	0.04	0.00
Sample size	7	3	9	10	27	37

This mechanism of quick brood reduction can be confounded by unusually slow growth of the A-chick after it hatches. In two natural broods both chicks survived past the B-chick's day 10; both chicks in each of these broods were still alive (at B-chick ages 42 and 73 days, respectively) when I left the colony for the season. HAs of these broods were 5 and 3 days, respectively, but both A-chicks grew slowly, in comparison with other A-chicks of the same year, until their siblings hatched (Fig. 4). Hatching Weight Ratios of these broods were 1.69 and 1.33, respectively, and were the seventh and second lowest of the 74 Hatching Weight Ratios measured during the 3 seasons.

Discussion

This study demonstrates that HA influences the timing of brood reduction in masked boobies, and that normal HA in this species ensures early siblicide. This mechanism fails only in rare cases when hatchling A-chicks grow unusually slowly. Other work on this population has demonstrated that a reliable mechanism to reduce the brood size to one chick increases chick growth rate and decreases the amount of parental care supplied to the brood (Anderson 1989b). In particular, parents of 20 day old matched nestmates (the normal nestling period is approximately 120 days (Nelson 1978)) feed their brood daily food masses equal

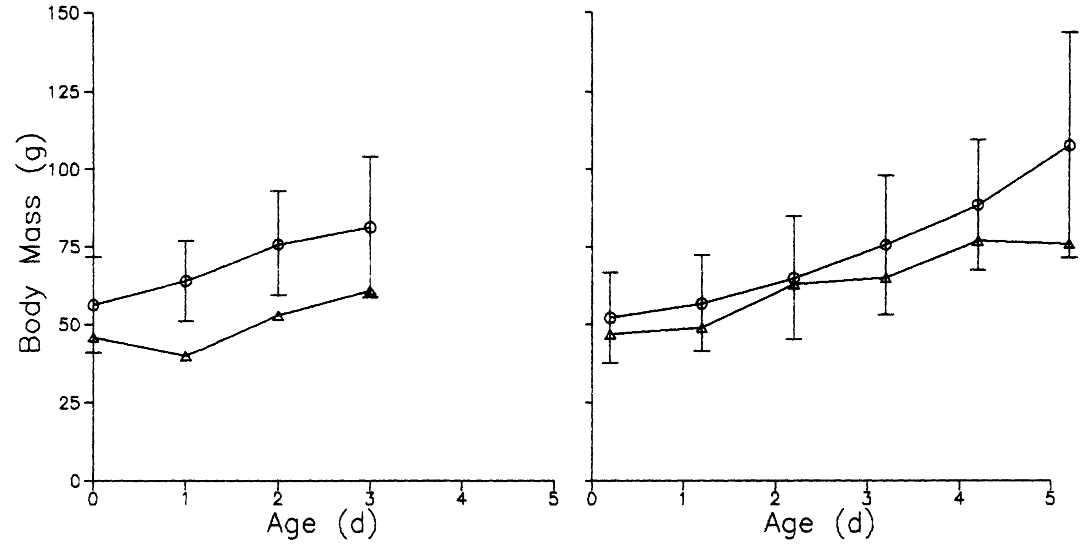

Fig. 4. Growth trajectories to the day of the b-chick's hatching of 2 masked booby A-chicks (triangles) that failed to kill their sibling (see text), in comparison with growth of all other A-chicks of the same year and HA (circles are means bracketed by 1 standard deviation)

to the peak demand of single chicks that occurs much closer to fledging (Anderson 1989b). Because pre-fledging brood reduction to a single chick is virtually inevitable, regardless of the degree of hatching asynchrony, due to sibling aggression (Nelson 1967), selection for such a reliable mechanism that avoids any cost, to parents and surviving offspring, of a larger brood is probably strong.

In accord with rest of the masked booby brood reduction system, HA is maintained above the apparent 3 day "early siblicide threshold". HA alone, however, cannot account for the different brood reduction systems of these two species. Blue-footed booby HAs generally fall at or just below the masked booby threshold, and blue-footed boobies would be expected to experience significant early brood reduction (see Table 2) if the two species differed only in HA. Blue-footed booby A-chicks may attack hatchling siblings (Nelson 1978, p. 565) and temporary ejections of B-chicks were observed during this study, but a suite of parental controls (including nest architecture and brooding behaviors as well as HA) prevents early mortality of B-chicks (Anderson, 1989b). Thus, differences in HA alone cannot account for differences in brood reduction in these two species.

The evolutionary basis of avian HA has been controversial because particular studies rarely support one hypothesis unequivocally. The association between variation in HA and brood reduction system presented here is similar to that of obligately (HA typically 3 day) and facultatively (HA typically 2 day) siblicidal eagles (Edwards and Collopy 1983), and, together with the result of the present study, is consistent with the adaptive Brood Reduction Hypothesis (Lack 1954) and not with variation predicted by other hypotheses for the evolution of HA (Hussel 1972; Clark and Wilson 1981; Hahn 1981; Mead and Morton 1985). However, the issue of how HA is controlled at the proximate level in siblicidal species remains largely unresolved. The period between ovulation and laying is apparently relatively fixed at approximately 24 h in most birds (Anderson et al. 1987). Thus, parents may have only two options for evolutionary adjustment of HA: spacing ovulations (Astheimer 1985) and commencing incubation (cf. Fujioka 1984). Data presented in Table 1 show how masked and blue-footed boobies may use these options. Laying asynchronies differ by approximately one day, and eggs are kept at incubation temperature beginning with the first egg's laying in masked boobies (HA is 96% of laying asynchrony), but after the first egg is laid (HA is 79% of laying asynchrony) in blue-footed boobies. The incubation patterns that produce proportionally shorter HA in blue-footed boobies are likely to be complex, because air and substrate temperatures in Isla Española colonies often equal or exceed normal incubation temperatures (Bartholomew 1966).

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