

## ORIGINAL ARTICLE

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**Parent blue-footed boobies suppress siblicidal behavior of offspring**

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**Abstract** Behaviorally dominant nestlings routinely kill sibling nestmates in blue-footed booby (*Sula nebouxii*) broods during periods of food shortage. Previous work demonstrated that these dominant, first-hatching “A-chicks” regulate the lethality of their behavior towards subordinate, second-hatching “B-chicks,” showing tolerance towards B-chicks except during chronic food shortages. Siblicide by A-chicks usually occurs after the hatchling stage. Results of an interspecific cross-fostering experiment indicated that A-chicks also attempt siblicide shortly after hatching, but parents apparently exert control over these attempts, and thwart them, when chicks are young. Theory predicts selection for such regulation in siblicidal birds that are likely to experience genetic parent-offspring conflict over the value of subordinant nestlings; our evidence of post-hatching parental regulation is consistent with that prediction.

**Key words** Siblicide · Brood reduction · Galápagos · Booby · *Sula* · Parent-offspring conflict

**Introduction**

Sibling competition in avian reproductive systems has attracted attention because it has obvious fitness consequences: competitively inferior offspring may receive less parental care and reach the end of parental care in poorer condition, or may even die. The latter case is referred to as brood reduction [partial brood loss (PBL) resulting from sibling competition, following Mock 1994]. In brood reduction, the behavior of competitively superior offspring thus directly influences parental reproductive success, raising the possibility of conflicts of

interest between parents and offspring as well as between offspring. Disagreement exists in the literature over whether the effects of sibling competition optimize parental reproductive success (the brood reduction hypothesis: Lack 1954, 1968; Ricklefs 1965; Mock 1994), are a major negative influence on parental fitness to be mitigated (the sibling rivalry reduction hypothesis: Hahn 1981), or are a minor correlated effect of adaptation in another sphere (e.g., Clark and Wilson 1981). In any case, we can expect such a dramatic influence on offspring survival to be regulated by parents, offspring, or both.

Three avenues of parental regulation have been proposed: manipulations of hatching interval (reviewed by Magrath 1990; Stoleson and Beissinger 1995), of egg size (e.g., Magrath 1992), and of egg hormone titer (Schwabl 1993, 1996; Schwabl et al. 1997). In this view, parents exert remote control of possible brood reduction; the post-hatching offspring competition occurs after the end of active parental manipulation of the offspring. We wish to emphasize the distinction between these pre-hatching manipulations of eggs and embryos (with indirect effects on sibling competition) and direct post-hatching behavioral regulation. Generally, parents are thought to leave the direct post-hatching regulation of competition to the offspring (Mock and Parker 1997), with rare exceptions (Spellerberg 1971; Stamps et al. 1987; Urrutia and Drummond 1990). One purpose of our paper is to question whether existing data justify this conclusion. However, we accept and rely on the premise that, given the existence of sibling competition and its fitness consequences, pre- and/or post-hatching parental regulatory mechanisms should be favored by natural selection. Existing field experiments support this premise (Mock and Ploger 1987; Amundsen and Stokland 1988; Osorno and Drummond 1995).

Siblicidal birds are dramatic examples of post-hatching offspring-based regulation of sibling competition. In these taxa, siblicide occurs when competitively dominant chicks “make a direct and significant contribution to the immediate death” (Mock 1994) of siblings,

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and parents are typically reported to play no active role. Regulation in the facultatively siblicidal blue-footed booby (*Sula nebouxi*) is conditional and complex. Behaviorally dominant A-chicks moderate their food intake during short-term food shortages, effectively redirecting food to subordinate B-chicks (Anderson and Ricklefs 1995). Conversely, during chronic food shortages A-chicks not only cease their clemency toward B-chicks, but launch ultimately fatal attacks on the sibling after reaching a characteristic level of poor condition (Drummond et al. 1986; Drummond and García Chavelas 1989).

O'Connor (1978) predicted the existence of genetic parent-offspring conflict (POC; Trivers 1974) over siblicide in birds. O'Connor noted that coefficients of relationship (sensu Hamilton 1964) differ and reasoned that, as food supply worsened, dominant offspring would favor a termination of parental care to subordinates under less stringent food limitation than would parents, causing a genetic conflict between parents and offspring. If offspring have the means to attempt siblicide, and parents have the means to resist, then a phenotypic conflict could arise over the fate of subordinate offspring at intermediate levels of food limitation. Well-adapted parents should be able to regulate siblicidal behavior, allowing it to proceed only when it serves their interests.

Dominant offspring of blue-footed boobies clearly have the ability to kill subordinate siblings, and do so as predicted during periods of food shortage (Drummond et al. 1986; Drummond and García Chavelas 1989). Direct, post-hatching parental attempts to regulate siblicidal behavior would be a logical expectation, but the apparent "hands-off" policy followed by parent blue-footed boobies after hatching is typical of descriptions of siblicidal bird taxa in general. The fact that siblicide is not accompanied by direct parental attempts to suppress the siblicide is congruent with recent theoretical results (Forbes 1993; Rodríguez-Gironés 1996) questioning the biological importance of genetic POC in the evolution of family interactions in birds. We wish to make the point that the *empirical* support for this position is weak, because the possible regulatory role of parents when siblicide does *not* happen is largely unstudied. Although this concern applies generally to post-hatching regulation of sibling competition, we will focus on the dramatic cost/benefit impacts of post-hatching regulation of siblicide.

Parental involvement in the successful regulation of sibling competition may be difficult or impossible to detect under natural conditions. To reveal any hidden parental regulatory effects, we took an experimental approach. We used a cross-fostering experiment between families of two booby species, the blue-footed booby and the masked booby (*S. dactylatra*), to partition the post-hatching regulatory influences of parents and offspring on sibling competition. Phylogenetic analyses show that these taxa are closely related (Warheit 1990; Friesen and Anderson 1996). This phylogenetic

affinity should act to control interspecific variance in evolving characters (e.g., Harvey and Pagel 1991). The two species have broadly similar foraging ecologies (Anderson 1989a; Anderson and Ricklefs 1992), breeding biologies (Nelson 1978), and they nest in adjoining colonies at our study site. The nest microenvironment in which hatchling chicks interact (see below) involves brooding on top of the parent's webbed feet and below the parent's feathered breast (no brood patch) in both species.

Obligately siblicidal masked boobies virtually always lose their second of two hatchlings to siblicide within days of hatching (Nelson 1978; Anderson 1989b, 1990a). In this "early" type of siblicide, the A-chick grabs the B-chick by the head, neck, or appendage and attempts to push the newly hatched B-chick from the nest scrape (see also Nelson 1978, p. 411). Early siblicide rarely occurs in blue-footed boobies, which also often hatch two chicks (Nelson 1978; Drummond et al. 1986; unpublished data 1984–1997). In the Galápagos Islands, deaths of hatchling blue-footed boobies are usually directly attributable to other factors, such as rain (Anderson 1995), and two siblings often fledge (Nelson 1978; unpublished data). Nonetheless, blue-footed booby chicks attack each other as hatchlings (Nelson 1978, p. 565; Anderson 1995; Osorno and Drummond 1995), and at older ages (Anderson and Ricklefs 1995; Osorno and Drummond 1995 and references therein). The behaviors exhibited by blue-footed booby A-chicks are similar to those of masked booby A-chicks (Anderson 1995). The critical difference that we exploited in our experimental design was that sibling aggression among hatchlings results in siblicide in one species but not in the other.

We constructed families with obligately siblicidal parents and facultatively siblicidal offspring and vice versa, for comparison with controls. We focused specifically on the 10 days after hatching of the second egg, which is the period of contrasting regulation of siblicide.

We tested the following hypotheses regarding the regulation of siblicide:

- (1) interspecific differences in the siblicidal tendencies of offspring can explain, by themselves, the interspecific difference between siblicide systems (the *nestling-influence hypothesis*);
- (2) interspecific differences in the suppressive tendencies of parents can explain, by themselves, the interspecific difference between siblicide systems (the *parental-influence hypothesis*);
- (3) interspecific differences in both offspring and parents are required to explain the interspecific difference between siblicide systems (the *joint-influence hypothesis*).

Contrasting predictions of these hypotheses are given in Table 1.

In addition, we used the data collected within blue-footed booby families to test the hypothesis that regulation of siblicidal brood reduction includes the active

**Table 1** Summary of predictions of hypotheses (*MB* masked booby, *BFB* blue-footed booby)

Treatment	Nestling-influence hypothesis	Parental-influence hypothesis	Joint-influence hypothesis
MB nestlings in BFB nest	Siblicide rate equals that of MB controls	Siblicide rate equals that of BFB controls	Siblicide rate intermediate to those of MB and BFB controls
BFB nestlings in MB nest	Siblicide rate equals that of BFB controls	Siblicide rate equals that of MB controls	Siblicide rate intermediate to those of MB and BFB controls

post-hatching suppression of siblicide. If any parental regulation was indicated by our results, that regulation would necessarily occur after hatching, because our cross-fostered families were created after hatching.

## Methods

We conducted reciprocal cross-fostering experiments at Punta Cevallos, Isla Española, Galápagos Islands, where both species nest, in December 1992 and January 1993. Details of the study site are given in Anderson and Ricklefs (1987). This period was the hatching peak for this relatively synchronously breeding masked booby population, and so was the best opportunity to obtain hatchling broods of this species. We monitored daily a pool of several hundred two-egg masked booby nests and 108 two-egg blue-footed booby nests, recording the dates of egg hatching. We identified broods of each species with two nestlings and the desired hatching interval (see below) on the day of the B-chick's hatching and either reciprocally transferred the broods for 15 days or left them unmanipulated as controls. A- and B-chicks are easily distinguishable within a brood by plumage development and wing chord until at least 55 days post-hatching (Anderson and Ricklefs 1995; A. Schwandt and D.J. Anderson, unpublished data), and we identified broodmates using these criteria.

The breeding adults in this experiment are parents of chicks in the experiment, but in some treatments are not the parents of the chicks that they cared for. To avoid confusion, we refer to the adults caring for a brood as the brood's "caregivers."

The degree of hatching asynchrony influences the probability and timing of siblicide (Anderson 1989b; Osorno and Drummond 1995), so we standardized the hatching interval by using intact natural broods that hatched at intervals of 3–5 days. The typical hatching spreads of these two species are 2–5 days for blue-footed boobies and 3–10 days (97% were 3–7 days) for masked boobies (Anderson 1989b). The 3- to 5-day range is the region of overlap of the two species' hatching intervals. This range includes both species' mean, median, and modal hatching interval. It includes over 50% of the hatching intervals of masked boobies and over 90% of the intervals for blue-footed boobies. Working with broods hatching at these intervals thus includes typical representatives of both species. All cross-fostered broods were returned to their home nests after 15 days.

Contemporaneous broods hatching at the required interval were randomly assigned to one of four treatments. Twenty broods of each species were reciprocally cross-fostered, and 17 blue-footed booby broods and 25 masked booby broods were left unmanipulated as controls. To control for the effect of cross-fostering itself, we compared the data from unmanipulated controls with those from *intraspecific* cross-fosters, using the same methods. Nest availability prevented us from establishing these controls in 1992–1993, so these *intraspecific* cross-fosters between 20 blue-footed booby and 22 masked booby broods occurred in 1995.

### Determining the cause of PBL

Early siblicide in natural masked booby broods follows a predictable sequence (Nelson 1978; Anderson 1989b). At our site, the

ejection event typically occurs over 1–2 min., and the ejected B-chick may remain outside the nest scrape, but within 20–100 cm of it, for several minutes to several days before death. Some victims are promptly removed by predators [Galápagos mockingbirds (*Nesomimus macdonaldi*) and frigatebirds (*Fregata* spp.)], and so may disappear without a trace in only moments. In other cases, the victim is within the defended space of the brooding parent; although the parent does not rescue the B-chick, it nonetheless prevents predators from removing the B-chick while it remains near the nest. As a result, victims may die of exposure and we sometimes observe these chicks during daily nest checks before they vanish. Ultimately, virtually all victims are removed from the nest site by predators or by scavengers [mockingbirds, frigatebirds, or crabs (*Grapsus grapsus*)] within a few days of ejection.

We monitored each nest daily during at least one brief visit (1 min), recording the number of live chicks present, any evidence of sibling aggression (displaced chick or bruises), and any information available regarding causes of PBL. We weighed the nestling(s) daily in all cross-fostered broods and in 10 unmanipulated blue-footed booby controls and in 11 unmanipulated masked booby controls.

When field schedules permitted, we conducted continuous daytime observations at nests to determine the cause of any PBL that occurred. The timing of breeding of the two booby populations required that the broods in our experiment be largely contemporaneous, but the spatial separation of our nests prevented the observation of more than one contemporaneous nest per observer at a time. The efficiency of our attempts to observe PBL events was further decreased by nighttime PBL in nests under observation, and because many broods under observation experienced no PBL.

### Alternative hypotheses for observed effects

The potential exists for artifactual effects of interspecific cross-fostering, if relevant variables went uncontrolled by our protocol. We evaluated two alternative hypotheses, beginning with the possibility that differential food intake by chicks amongst caregiver categories could cause differences in PBL among treatment groups.

Adult boobies regurgitate to their hatchlings a soupy mix of predigested prey items, and the hatchling's head is inserted well into the parent's mouth during feeding. Feedings occur in both daylight and at night (Anderson and Ricklefs 1992). These circumstances complicate studies of the amount of food transferred per unit time. In other studies, we have used weighings at 4-h intervals to estimate 24-h food intake by booby nestlings (Anderson 1990b, Anderson and Ricklefs 1992), but not for hatchlings because separating a hatchling from the parent every 4 h for weighing, especially at night, causes an unacceptable level of disturbance.

Nestling food intake is positively related to body mass after the hatchling stage in both species (Anderson and Ricklefs 1992). We assume here that this relationship exists during the hatchling stage also, which would mean that hatchlings require much less food ( $\ll 120$  g) than adults of either species are capable of supplying (Anderson and Ricklefs 1992). No nestling in this experiment reached 750 g by 15 days post-hatching age, and at that mass, per capita daily food intake is approximately 140 g for nestlings of both species (Anderson and Ricklefs 1992). Doubling this demand (280 g/day) for a two-nestling brood would far exceed any brood's demand during this experiment, yet we have demonstrated elsewhere that parents of both species are capable of satisfying even this demand (Anderson 1990b; Anderson and Ricklefs 1992).

Parental feeding is “essentially similar” in booby species (Nelson 1978, p. 948), and we saw no evidence of behavioral problems that might impede food transfer in heterospecific families. Nonetheless, we examined the possibility of such feeding difficulties by comparing the masses (ages 5, 10, and 15 days) of control and cross-fostered A-chicks in a repeated-measures ANOVA.

It is also possible that aspects of food supply differed across species in a manner that triggered the hunger-dependent siblicide shown by older blue-footed booby nestlings (Drummond et al. 1986; Drummond and García Chavelas 1989). If this was so, then differences among treatment groups could be attributed to more serious food limitation at masked booby nests, coupled with hunger-dependent siblicide in hatchlings of both species. We tested this hypothesis using body mass data in a paired *t*-test, comparing the mass of a siblicidal A-chick with masked booby caregivers with that of a non-siblicidal, time- and age-matched A-chick with blue-footed booby caregivers.

Another potentially confounding factor could be hatching interval, since it influences the outcome of sibling competition amongst hatchling masked boobies (Anderson 1989). In our experimental design, we formed a pool of broods with 3- to 5-day hatching intervals, and randomly assigned broods from the pool to one of the four treatments. We tested for differences in hatching interval with a two-way ANOVA, with parent species and treatment as effects.

All statistical analyses were performed using Statistica v.4.5 for Windows. We followed the recommendation of Zar (1984) to analyze  $2 \times 2$  contingency tables with Fisher’s exact test since some cells contained zero. All reported *P*-values are from two-tailed tests.

## Results

### PBL after intraspecific transfers

No PBL occurred by the B-chick’s 15th day in 20 intraspecifically cross-fostered blue-footed booby broods; PBL occurred in all 22 intraspecifically cross-fostered masked booby broods. In addition, the B-chick’s age at disappearance in masked booby broods did not differ across controls (Mann-Whitney  $U = 218$ ,  $n_1 = 25$ ,  $n_2 = 22$ ,  $P > 0.05$ ; median = 3 days in both cases).

### PBL after interspecific transfers

No A-chick of either species died during the experiment, while 49 B-chicks (60%) did. In three cross-fostered broods, we observed the brood reduction event, and in

each case the A-chick ejected the B-chick from the nest scrape and the B-chick died near the nest scrape from exposure or attacks by Galápagos mockingbirds. We thus classify these events as siblicide. Two of the observed siblicides occurred among blue-footed booby chicks in a masked booby nest. The third occurred in a masked booby brood cross-fostered to a blue-footed booby nest. In a fourth cross-fostered masked booby brood we observed the A-chick attacking and attempting to eject its sibling on two different occasions, but in both cases, the B-chick managed to return to the scrape. This B-chick disappeared by the following day.

In one of the above-mentioned broods, the B-chick had red marks on its head and neck caused by its sibling’s attacks. We noted similar marks on seven other cross-fostered B-chicks that later disappeared, but not on any chicks that did not disappear. We noted four cross-fostered B-chicks just outside the nest scrape, near death or dead, while the rest of the family was intact. In the other cases of PBL in our experiment, the hatchling B-chick simply disappeared. These data all indicate that siblicide was the cause of PBL in this experiment.

The proportion of B-chicks that died depended on the treatment (Table 2). Victims of siblicide showed two risk factors: masked booby caregivers and/or a masked booby nestmate. At masked booby nest sites, siblicide occurred at a significantly higher rate among masked booby nestlings than among blue-footed booby nestlings (Table 3, contrast A); the same was true at blue-footed booby nest sites (Table 3, contrast B). This result permits rejection of a pure parental-influence hypothesis that interspecific differences in parental characteristics can explain, by themselves, the natural difference in siblicide systems, since caregiver species was controlled within each of these two contrasts.

When masked booby nestlings had masked booby caregivers, siblicide was significantly more likely to occur than if they had blue-footed booby caregivers (Table 3, contrast C); the same was true for blue-footed booby nestlings (Table 2, contrast D). This result permits rejection of a pure offspring-influence hypothesis that interspecific differences in offspring behavior can explain, by themselves, the natural difference in siblicide systems, since nestling species was controlled within these contrasts. This is a key result: aspects of the par-

**Table 2** Fates of B-chicks by treatment, to age 15 days (*MB* masked booby, *BFB* blue-footed booby)

B-chick fate	MB nestlings with MB parents	MB nestlings with BFB parents	BFB nestlings with MB parents	BFB nestlings with BFB parents
Lived	0	4	12	17
Disappeared (no trace)	23	10	5	0
Outside nest				
Consistent with siblicide	2	5	1	0
Siblicide witnessed	0	1	2	0
Total dead (all consistent with siblicide)	25	16	8	0
Proportion dead	1.00	0.80	0.40	0.00
<i>n</i>	25	20	20	17

**Table 3** Probabilities of early siblicide contrasted by treatment. All Fisher's exact tests are two-tailed (*MB* masked booby, *BFB* blue-footed booby)

Contrast		No siblicide (B-chick lived)	Siblicide (B-chick died)	<i>n</i>	Fisher's exact test ( <i>P</i> )
Contrasts with parent species controlled					
A	MB nestlings with MB parents	0	25	25	< 0.01
	BFB nestlings with MB parents	12	8	20	
B	MB nestlings with BFB parents	4	16	20	< 0.01
	BFB nestlings with BFB parents	17	0	17	
Contrasts with offspring species controlled					
C	MB nestlings with MB parents	0	25	25	0.03
	MB nestlings with BFB parents	4	16	20	
D	BFB nestlings with MB parents	12	8	20	< 0.01
	BFB nestlings with BFB parents	17	0	17	

ents, or of the nest site that they prepare (Anderson 1995), influence the probability of siblicide. Blue-footed booby parents/sites restrict early siblicide, while those of masked boobies facilitate it.

The timing of masked booby siblicide provides further evidence of the effect of caregiver species on nestling aggression. When masked booby siblicide did occur in blue-footed booby nests, it was delayed relative to control broods by 3 days (Mann-Whitney  $U = 19$ ,  $n_1 = 16$ ,  $n_2 = 10$ ,  $P < 0.01$ ).

#### Tests of alternative hypotheses

Differential food intake by chicks amongst caregiver categories could explain these results if chicks with masked booby caregivers received lower-quality food or less food than with blue-footed caregivers. Diet composition, estimated using induced regurgitations, was similar for these species during this study: 88% of 298 masked booby prey items from 58 birds were sardines (*Sardinops sagax*), as were 98% of 131 blue-footed booby prey items from 20 birds (unpublished data). The remaining items in both diets were *Exocetid* flying fish and *Scorbrid* mackerels.

We applied a repeated-measures ANOVA to body mass data to test the hypothesis that food availability differed between caregiver treatments. The effects of interest were treatment and age  $\times$  treatment interaction. The age effect was highly significant in all of the analyses ( $P \ll 0.01$ ); that is, nestlings increased in mass as they increased in age. For masked booby chicks, the treatment effect was not significant ( $F_{1,29} = 0.21$ ,  $P > 0.05$ ), although the age  $\times$  treatment interaction was ( $F_{2,58} = 3.58$ ,  $P < 0.05$ ). This significant interaction indicates slower growth of cross-fostered masked booby chicks with blue-footed booby caregivers, in which siblicide was suppressed at the youngest ages. When we repeated the analysis, including only broods from which the B-chick was lost, neither the treatment effect ( $F_{1,26} = 0.52$ ,  $P > 0.05$ ) nor the interaction effect ( $F_{2,52} = 2.14$ ,  $P > 0.05$ ) were significant. This result indicates that chick food intake with masked booby caregivers was not lower and so cannot explain the higher mortality with

masked booby caregivers. The same was true for blue-footed booby chicks: neither the treatment effect ( $F_{1,28} = 2.03$ ,  $P > 0.05$ ) nor treatment  $\times$  age interaction ( $F_{2,56} = 1.54$ ,  $P > 0.05$ ) were significant.

It is possible that aspects of food supply differed across species in a manner that triggered the hunger-dependent siblicide shown by older blue-footed booby nestlings (Drummond et al. 1986; Drummond and García Chavelas 1989). This explanation would require more serious food limitation with masked booby caregivers than with blue-footed booby caregivers, which we have already rejected. It would also require a conditional response to food limitation by hatchlings of both species, yet masked booby hatchlings have shown no indication of a conditional siblicidal response to food limitation in the 14 years that we have studied them. Finally, hatchlings that lost a sibling in this experiment were not in poorer condition than those whose sibling survived. Eight blue-footed booby A-chicks with masked booby caregivers lost their sibling; six had higher masses on the day of the sibling's death than did their matched control, and the mean mass of experimentals on the day of the sibling's death (175.0 g, SD = 92.9) did not differ from that of matched controls (160.6 g, SD = 90.0; paired  $t = 0.74$ ,  $df = 7$ ,  $P > 0.05$ ). Similarly, all four masked booby A-chicks with blue-footed booby caregivers whose sibling survived had lower masses than their time- and age-matched controls in masked booby nests. The mean mass of the A-chicks on the day of brood reduction (127.3 g, SD = 32.8) exceeded that of the matched controls (105.8 g, SD = 28.4; paired  $t$ -test  $t = 4.65$ ,  $df = 3$ ,  $P < 0.05$ ). In these cases, the A-chicks involved in brood reduction were not in worse condition than matched controls without brood reduction.

In spite of the random assignment of chicks, slight differences existed in hatching intervals between some treatments. A two-way ANOVA of hatching interval, with parent species and treatment as effects, showed significant parent ( $F_{1,78} = 10.41$ ,  $P < 0.01$ ) and parent  $\times$  caregiver interaction effects ( $F_{1,78} = 10.82$ ,  $P < 0.01$ ), but no caregiver effect ( $F_{1,78} = 0.13$ ,  $P > 0.05$ ). Inspection of treatment means showed that hatching intervals of broods with blue-footed booby caregivers

were nearly identical (masked booby broods mean = 4.05 days, SD = 0.51; blue-footed booby broods mean = 4.05 days, SD = 0.66). The significant effects were due primarily to differences between broods with masked booby caregivers (masked booby broods mean = 4.56 days, SD = 0.65; blue-footed booby broods mean = 3.65 days, SD = 0.67).

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## Discussion

### Patterns of PBL

The observed PBL in the manipulated controls fit the described patterns for unmanipulated broods (Anderson 1989b), and they match the data from unmanipulated controls in this study (Table 2). Although it was not possible to run the two types of controls in the same year, the total agreement between these two controls, and between the controls and all of our non-experimental data on the breeding biology of these species, gives us confidence that the controls did not differ within species. Therefore, we conclude that the procedure of cross-fostering itself did not influence the outcome of the experiment.

Despite the problems associated with monitoring nests for brood reduction, we recorded three cases of siblicide. All of the other cases of PBL recorded in this experiment were consistent with the scenario that PBL was a result of brood reduction. The chick behavior and sequence of events in each case was typical of normal masked booby “early” siblicide; it is therefore noteworthy that two of the observed siblicides occurred among blue-footed booby chicks in masked booby nests. Indirect evidence, including marks on the back of the B-chicks’ head implicates early siblicide as the cause of PBL in several other cases. Our experience with these species at this site since 1984 has shown that only ejection by the A-chick can account for the cases of chicks located just outside the nest scrape while the rest of the family was intact. In the other cases of PBL where the chick just disappeared, we saw nothing to contradict the interpretation that siblicide by ejection from the scrape was the cause.

We know of no mortality factor other than siblicide that can account for the disappearance of a hatchling B-chick from the nest of either of these species. We have never observed any parent booby removing either a live or dead chick from a nest. Potential predators of hatchlings in the nest are Galápagos hawks (*Buteo galapagoensis*; these frequently take older chicks not attended by parents; Anderson 1991; Anderson and Hodum 1993), short-eared owls (*Asio flammeus*, reported to take older chicks; Nelson 1978), mockingbirds, frigatebirds, *Grapsus* crabs, and snakes (*Dromicus biserialis*). We have never seen snakes in the vicinity of a booby nest, although we frequently see them elsewhere on the island. The other potential predators are excluded

from the vicinity of nests of both species by attending parents, and we suspect that the snake would be also. Thus, depredations of hatchlings in the nest could occur only if parents were absent from the nest, but at least one parent was always present at the nests during this experiment.

The remaining circumstance in which B-chicks die occurs occasionally in natural nests in both species: B-chicks die in the nest, not outside it. These corpses remain in the nest and are trampled into the substrate. However, this did not happen at any of the nests in our experiment.

In summary, only B-chicks died in PBL events: in some cases, siblicide was known to be the cause of PBL; in some others, circumstantial evidence strongly implicated siblicide as the cause, and in the remaining cases, the circumstantial evidence surrounding the PBL was totally consistent with siblicide as the cause, and inconsistent with any other plausible cause. Therefore, we are confident that brood reduction, specifically siblicide, was the cause of all of the PBL documented in this study.

### Evaluation of alternative hypotheses

Booby chicks in all treatments and controls gained mass with age. The insignificant ANOVA main effects and interactions indicate that mass gain and, by implication, food provided by parents did not differ for masked or blue-footed booby chicks across caregiver species. In addition, siblicidal offspring were not in worse condition than matched non-siblicidal controls, so the differences associated with caregiver species cannot be attributed to low food provisioning by masked booby adults. Additionally, it is possible that these species differ in diet quality (resulting, perhaps, from different prey composition of food delivered to the chick) which could (at least partially) explain the differences in rates of PBL. However, data from this field site show that the two species have broadly similar diets (Anderson 1989a, unpublished data). Thus we reject the hypothesis that some aspect of the food supply explained the observed patterns of brood reduction.

Finally, we evaluated the hypothesis that differences in hatching interval explain the observed differences in brood reduction. We found that the hatching intervals of broods with masked booby caregivers differed slightly: the hatching interval of blue-footed booby broods was about 1 day less than that of masked booby broods. The main effect of this bias on the results in Table 3 would be on contrast A, and the effect, if any, would be to underestimate the frequency of siblicide in the blue-footed booby broods. It is unlikely that we overestimated the frequency of siblicide of the masked booby broods in masked booby nests, as the natural condition is obligate siblicide. The magnitude of the bias should be related to the difference (approximately 1 day) in hatching interval. In Fig. 3 of Anderson (1989b),

which relates hatching interval to B-chick age at death, this difference in hatching interval in masked boobies would have led to a change in timing, but not probability, of siblicide of approximately 1 day during a 15-day experimental trial. This effect is minor compared to the magnitude of the effect detected in contrast A ( $P < 10^{-5}$ ). We have no way to correct this bias, but in any case it was unlikely to affect our results in a qualitative way.

#### Parental and offspring effects in the frequency of brood reduction

Both parents and offspring influence the probability of siblicide in these species; in particular, parents have a post-hatching influence that varies between species. Our results indicate that parent masked boobies and their A-chick jointly facilitate the demise of the family's B-chick; dynamics within blue-footed booby families are more complex. Among blue-footed boobies, it appears that parents and A-chicks exert opposing influences on the B-chick's fate shortly after hatching, and that parents typically prevail (see Table 3, contrast D). The aggressive behavior between hatchling blue-footed booby chicks was not unexpected, even though it does not normally cause siblicide, because such behavior had been noted in normal blue-footed booby broods (Anderson 1995). In those instances, the steep sides of the nest scrape seemed to prevent the aggression from causing an ejection. Displaced B-chicks were returned to the brooding location under the parent by rolling down the sides of the nest (Anderson 1995).

The evidence of a cross-fostering effect in this experiment is a more novel result. We have tried unsuccessfully to account for the data in Table 2 as experimental artifacts, and so we have concluded that the variation induced by cross-fostering is in part a result of variation in parental regulation of sibling aggression. The effect is behaviorally subtle, since no overt post-hatching conflict between parents and offspring has been observed in non-experimental broods of this species by us or other workers (Drummond et al. 1986; Drummond 1987). We are currently working to identify post-hatching parental traits that suppress siblicide.

Earlier, we made the point that the regulatory role of parents when siblicide does *not* happen is largely unstudied and possibly unappreciated. Blue-footed boobies present an object lesson in this respect. Prior to this experiment, it was known that at least some ejection-type behavior occurred between hatchling blue-footed boobies (Nelson 1978, p. 565; Anderson 1995; Osorno and Drummond 1995), but that it did not lead to actual ejections. The data in Table 2 suggest that approximately half of blue-footed booby A-chicks attempt to eject their hatchling sibling and half do not (see blue-footed booby broods with masked booby care-takers). One can infer from these data on apparently unregulated chicks that when early siblicide does not occur in natural

families of this species, approximately half of those non-events are due to failure of the A-chick to attempt siblicide, and the other half are due to potential ejections that were unsuccessful due to the influence of the parents.

The operative aspect of our experiment was to either remove a putative regulatory mechanism and determine if the offspring then became unregulated (blue-footed boobies in masked booby nests), or to impose a putatively regulated environment on offspring and determine if the offspring then became regulated (masked booby broods in blue-footed booby nests). We can envision similar applications of this approach to other parent-offspring associations in which parental regulation of sibling competition may be cryptic. Brood division, in which the newly fledged brood members split into two groups, each group accompanying only one parent, may be a mechanism to reduce the effects of competition. If so, that parental regulatory mechanism could be removed by confining experimental captive families such that all fledglings competed as a group; control families could be confined to a similar volume of space, but with the space divided to prevent consolidation of the brood. Cross-fostering experiments such as the one we conducted provide another attractive approach, but it may be rare to find closely related, co-occurring taxa that differ in aspects of sibling competition.

O'Connor's (1978) theoretical analysis of POC over avian brood size predicted parental interference in siblicide. Our results are consistent with this prediction, and so constitute rare evidence of a systematic effect of this kind. We recognize the paradox posed by blue-footed booby nestlings, which may attempt to kill their subordinate sibling early in the nestling period if permitted to do so (this paper), when food demand is low, yet show apparent kin-selected tolerance of the same sibling a few weeks later, when food demands have risen (Drummond et al. 1986; Drummond and García Chavelas 1989; Anderson and Ricklefs 1995). Information at the ultimate level will be required to evaluate the ability of the POC hypothesis to resolve this paradox. If POC exists early in the nestling period and not later, then the value of the B-chick to the A-chick must switch during the nestling period from negative to positive.

Our goal in this paper was to test O'Connor's (1978) prediction in an appropriate model system; we recognize, however, that other interpretations of our results are possible. While consistent with O'Connor's POC hypothesis, our data do not exclude a hypothesis alternative to POC, that the behavior causing early siblicide in our experimental blue-footed booby broods is an epiphenomenon correlated with the expression of normal, later siblicide. Since parental regulation prevents the behavior from leading to siblicide, the character may have little or no cost early in the nestling period and could be pleiotropically associated with adaptive aggressive behavior later in the nestling period. It is also possible that the behavior is in fact adaptive even though

it seldom leads to siblicide, if the behavior contributes to future dominance status via behavioral conditioning of the B-chick (Drummond and Osorno 1992) or learning of aggressive behaviors by the A-chick. These hypotheses can all be investigated with appropriate experimental design, and we agree with Mock and Forbes (1992) that a robust evaluation of the evolutionary impact of POC on breeding biology will require experimentation combined with a multi-hypothesis approach to the study of parent-offspring interactions.

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