# THE ROLE OF PARENTS IN SIBILICIDAL BROOD REDUCTION OF TWO BOOBY SPECIES

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ABSTRACT.—Parental regulation of the probability and timing of avian brood reduction is expected to exist and evolve because natural selection should favor parents that match brood size to food availability most efficiently. Since food availability varies among species, interspecific variation in this regulation is expected. Comparative study of species with different brood reduction systems is one way to test the hypothesis that these mechanisms evolve as adaptations. Previous work on obligately siblicidal Masked Boobies (*Sula dactylatra*) and facultatively siblicidal Blue-footed Boobies (*S. nebouxii*) has shown that their different hatching asynchronies cannot fully explain the qualitative difference in their brood reduction systems. In this study, I report interspecific differences in nest shape that appear to contribute to early siblicide in Masked Boobies, but that suppress early siblicide in Blue-footed Boobies. Blue-footed Booby nest shape is closely regulated by parents. Differences in egg sizes of nest mates do not appear to contribute to the difference in social systems. *Received 19 January 1995, accepted 2 July 1995.*

FATAL SIBLING AGGRESSION, known as "siblicide," often reduces the brood size of a number of bird species (Stinson 1979, Mock et al. 1990). Lack's (1954) brood-reduction hypothesis is the basis for the common evolutionary interpretation of siblicide, and of brood reduction (Ricklefs 1965) in general. When food supply for nestlings cannot be predicted reliably at the time of laying, selection is expected to favor a strategy of hatching as many nestlings as can be raised in the best conditions, and then of eliminating nestlings after hatching, if necessary, to bring demand into line with supply (see also Temme and Charnov 1987, Forbes and Ydenberg 1992). Siblicide provides parents an optimizing tool with a notable advantage: individual nestlings are best able to gauge their own physiological condition and can use that information, in conjunction with a competitive hierarchy, to maximize efficiency of brood reduction (Mock et al. 1987a).

Reliance on dominant offspring to conduct siblicide also carries a notable disadvantage. Offspring may commit siblicide under less-stringent conditions than is optimal for parents, especially if parent-offspring conflict exists (Trivers 1974, O'Connor 1978, Dickins and Clark

1987). Thus, parents may benefit from regulating siblicide. Specifically, they are expected to have experienced natural selection for regulatory mechanisms that rank offspring for survival within a competitive hierarchy, but suppress siblicide that is not in the parents' best interests. Whether the first or second objective is emphasized during selection will depend on the extent of brood reduction that is optimal for parents, and is expected to vary across species.

Past interest has focused on two mechanisms to regulate sibling competition. Variation in the interval between successive hatchings of nest mates (hatching asynchrony) and in egg size explain much of the variation in competitive ability within a brood (Ricklefs 1965, Parsons 1970, 1975, Hahn 1981, Braun and Hunt 1983, Slagsvold et al. 1984, Hebert and Barclay 1986, Ploger and Mock 1986, Skagen 1987, Amundsen and Stockland 1988, Hebert and Barclay 1988, Anderson 1989a, Magrath 1992, Jover et al. 1993), with hatching asynchrony being the more important (Stokland and Amundsen 1988, Magrath 1992). In species with sibling aggression, available evidence shows that food distribution parallels the competitive hierarchy within the brood (Poole 1979, Braun and Hunt 1983, Fujioka 1985, Inoue 1985, Mock 1985, Cash and Evans 1986, Drummond et al. 1986, Hagen 1986, Ploger and Mock 1986). Parents create a com-

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petitive hierarchy and, by not distributing food counter to the hierarchy, reinforce it through positive feedback.

Only rarely have comparative studies tested the hypothesis that differences between species in siblicidal phenomena are explained by differences in regulatory mechanisms. Ideally, such studies should compare species that differ in outcome of sibling competition, they should focus on interspecific variation in traits known to influence competitive hierarchies, and they should eliminate to the extent possible confounding effects of phylogenetic and ecological dissimilarity. Two studies have compared the hatching asynchronies of obligately siblicidal eagles (Edwards and Collopy 1983) and boobies (Anderson 1989a) with those of facultatively siblicidal congeners. Longer hatching asynchronies (presumably under at least partial control of parents) give greater competitive advantage to elder chicks of many siblicidal species (see above); both studies found that hatching asynchronies of obligately siblicidal species were longer than those of facultatively siblicidal congeners. Mock and associates found that the degree to which food delivered by parents can be monopolized explains variation between two ardeid species in the probability of siblicide (Mock 1984, 1985, Mock et al. 1987a, Mock et al. 1987b); however, whether parents actively manipulate food monopolizability as a regulatory mechanism is unknown.

In this study, I present comparative data from two siblicidal booby species of potential influences of sibling aggression. My goal is to identify mechanisms that parents use to regulate the outcome of sibling aggression, and to test the hypothesis that differences in regulatory mechanisms contribute to differences in the social systems of these species.

## THE STUDY SYSTEM

Masked Boobies (*Sula dactylatra*) and Blue-footed Boobies (*S. nebouxii*) are colonial, ground-nesting, piscivorous seabirds that breed sympatrically throughout most of the Blue-footed Booby's range (Nelson 1978). Blue-footed Boobies lay one to four eggs per clutch (usually two) and are facultatively siblicidal; first-hatched chicks ("*A*-chicks") kill younger siblings in times of food stress (Drummond et al. 1986, Drummond and Garcia Chevelas 1989). Nonetheless, more than one offspring often (Nelson 1978) or usually fledge (66% in case of Drummond et al. 1986). Masked Boobies lay one- or two-egg clutches, and are obli-

gately siblicidal. If both eggs hatch, the *A*-chick ejects the second-hatched chick ("*B*-chick") from the nest scrape, and the victim dies from exposure or predation. The timing of siblicide also differs; the average age at death of victim Blue-footed Boobies is 18 days (Drummond et al. 1986), while that of Masked Booby victims is 1.8 days (Anderson 1989a). Masked Booby parents are prevented from fledging two offspring by unrelenting sibling aggression (Nelson 1978, Anderson 1989a); the insurance value of the second egg against the first egg's failure to hatch apparently explains why they lay two eggs (Dorward 1962, Anderson 1990a). Some data suggest that parent Masked Boobies could provide enough food for two surviving nestlings (Anderson 1990b, Anderson and Ricklefs 1992), but *A*-chicks do not permit parents to try. Even if the parents could suppress siblicide behaviorally, both parents are absent from the nest site for up to 8 h daily in experimentally-managed two-chick broods (Anderson 1990b). During these periods a subordinate has no protection from its sibling's attacks. Parents avoid investing in a doomed offspring and *A*-chicks expend less effort when siblicide occurs shortly after hatching of the *B*-chick.

A previous experimental study showed that the degree of hatching asynchrony influenced the probability and timing of siblicide in Masked Boobies (Anderson 1989a). Broods hatching at intervals of at least 4 days virtually always lost the *B*-chick within 20 days (total nestling period ca. 100 days); the average time to brood reduction was 1.8 days. Early brood reduction became increasingly unlikely as hatching asynchrony was decreased from three to one days in experimental broods. As expected under the "doomed-offspring" scenario above, the mean hatching interval in Masked Booby broods was 5.4 days (range 3–10 days), above the "early reduction threshold" (Anderson 1989a) of 3 days. Anderson (1989a) also showed that hatching intervals of Blue-footed Boobies ($\bar{x}$ = 3.5 days) were significantly shorter than those of Masked Boobies, but that more than 50% of Blue-footed Booby broods hatched at intervals exceeding the three day early reduction threshold. A Masked Booby *B*-chick hatches four days after its sibling and can expect to be killed within three days of hatching. However, a Blue-footed Booby *B*-chick in a similar situation in the Galápagos will probably fledge, if it escapes predators (Anderson 1989a, 1991, Anderson and Hodum 1993) and bad weather (this paper). The degree of hatching asynchrony is the primary regulatory variable investigated in studies of avian sibling competition, but it cannot explain the qualitative difference between the social systems of these two siblicidal species.

A Masked Booby *A*-chick ejects its sibling by grasping in its beak the sibling's neck, appendage, or skin and extending its neck to thrust the *B*-chick across the nest scrape. Then, an *A*-chick often repeats the thrust after moving its own body 2 to 10 cm toward

the displaced B-chick. A series of thrusts often moves the B-chick from the shade cast by the parent. Behavioral data, both observational (Nelson 1978:565, this study) and experimental (Lougheed 1995), show that hatchling Blue-footed Booby A-chicks display the same behavior, but at lower frequency and without lethal outcome. Experimental cross-fostering of chicks of one species into nests of the other species demonstrated that both parents and chicks play regulatory roles vis-a-vis expression and outcome of sibling aggression (Lougheed 1995). In the present study, I focus on parental influences that facilitate the B-chick's ejection in Masked Booby broods and suppress it in Blue-footed Booby broods.

## MATERIALS AND METHODS

Data presented here were collected from 1984 through 1986 as part of a long-term study of the breeding ecology and behavior of Masked and Blue-footed boobies at Punta Cevallos, Isla Española in the Galápagos Archipelago (for details of study site, see Anderson and Ricklefs 1987). This period fell between the El Niño-Southern Oscillation events of 1982–1983 and 1986–1987 (Anderson 1989b). My assistants and I recorded nest histories and measured chick growth of approximately 250 Masked Booby and 100 Blue-footed Booby breeding attempts in each season. We checked nests daily between 1200 and 1430, marked newly laid eggs, and weighed and measured chicks daily until the age of 10 days. We measured the maximum length and breadth of each egg, and approximated the egg's volume with the equation

$$V = \pi L B^2 / 6,   \qquad (1)$$

where $V$ is volume (cc), $L$ is length (cm), and $B$ is breadth (cm; Preston 1974). We measured chick masses with Pesola spring scales; wing length was measured by holding the metacarpals at a right angle to the radius and ulna, and straightening the manus or longest primary. The A- and B-chicks were individually identified using ink spots we placed on the head, plumage development, and, after about 30 days of age, their U.S. Fish and Wildlife Service aluminum leg bands. I excluded from analyses presented here three three-egg Blue-footed Booby clutches, and two Masked Booby broods in which brood reduction did not occur by 20 days after the B-chick hatched (see Anderson 1989a).

A chick was recorded as hatched at a given midday nest check when the chick was completely outside its egg shell, or the chick was still attached to the egg shell but had split the egg shell into two halves. Brood reduction was recorded when a chick was absent from its nest scrape at a particular day's nest check and, subsequently, did not return; frequently, chicks of both species returned to their nest scrape after being recorded outside the scrape as a result of sibling ag-

gression or of their own disorientation. Thus, hatching asynchrony and time required for brood reduction were measured in increments of one day.

Both species lay their eggs directly on the ground in circular nest scrapes that have been cleared of debris. I measured the diameters of 75 Blue-footed Booby and 45 Masked Booby nest scrapes by placing a meter stick across the scrape at its maximum diameter and recording the distance between points of contact with the ground. A second measurement was made horizontally perpendicular to the first, and the average of the two was taken as the nest's diameter. The maximum depth was measured at the center of the scrape with another ruler held perpendicular to the horizontal meter stick. The nest scrape's maximum steepness ($\Gamma$, the angle in degrees made by horizontal plane and tangent to surface of scrape where surface nears ground level) is approximated by

$$\Gamma = 180° - 2[\tan^{-1}(R/D)],   \qquad (2)$$

where $R$ is the radius (cm) and $D$ is the maximum depth (cm; see Appendix for a proof).

Statistical analyses were done with SYSTAT (SYSTAT, Inc. 1984), CSS:STATISTICA (StatSoft, Inc. 1991), and STATISTICA (StatSoft, Inc. 1994) software. Stepwise multiple regressions of dependent variables on hatching interval and egg-volume ratio attempted to include hatching interval in the model first, at $\alpha$-to-enter $= 0.15$, where $\alpha$ is determined by an independent variable's $t$-value (e.g. Neter and Wasserman 1974: 386).

## RESULTS

*Egg-volume differences.*—Variation in egg size explains significant variation in the posthatching growth rate of some bird species, and differences in egg size within a clutch could influence the outcome of siblicidal behavior through an effect on body-size difference (Anderson 1989a). To do so, egg volume must influence body size. In order to explain interspecific differences in siblicidal behavior, the two species must have different egg-volume ratios. Egg volume explains 46.4 and 50.9% of variation in hatching mass of Masked and Blue-footed boobies, respectively, and the effect decays with increasing age but remains significant at least through eight days of age (Table 1). Egg-volume ratios (i.e. volume A-egg/volume B-egg) of the two species differ in association with the brood-reduction system: Masked Booby A-eggs usually were larger than B-eggs (Anderson 1990a), while 24.4% of Blue-footed Booby A-eggs were the smaller of the two (Fig. 1, Table 2). A two-way ANOVA, with species and year as main
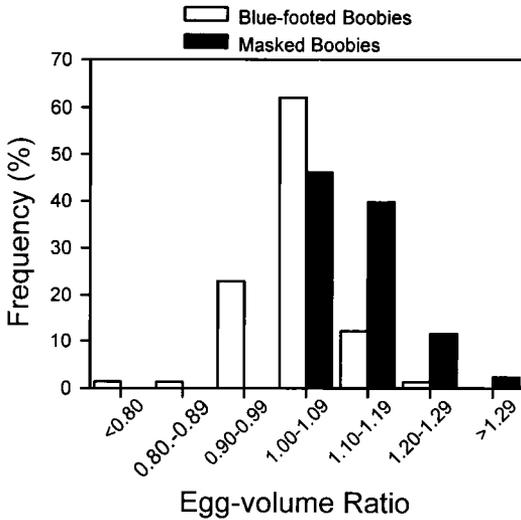
Fig. 1. Frequency histogram of egg-volume ratios (volume of A-egg/volume of B-egg) for Masked ($n = 171$) and Blue-footed ($n = 74$) booby clutches.

effects, revealed a significant species effect ($F_{1,239} = 24.91, P < 0.001$). Masked Boobies had a larger mean egg-volume ratio than did Blue-footed Boobies ($\bar{x} = 1.11 \pm$ SD of 0.11, and $\bar{x} = 1.03 \pm$ of 0.07, respectively; see Table 2).

Hatching interval explains significant variation in the ratio of the A-chick's mass to the B-chick's mass on the day of the B-chick's hatching (hatching-mass ratio; $r^2 = 0.41$ for Masked Boobies, $r^2 = 0.39$ for Blue-footed Boobies; Anderson 1989a). Stepwise multiple regression of

TABLE 1. Proportions of variance ($r^2$-values) in body size (as indicated by mass or wing length) explained by variation in egg size. Only A-chicks from two-egg clutches used so as to minimize variation due to parent quality.

| Age (days) | Masked Booby | | Blue-footed Booby | |
|---|---|---|---|---|
| | Mass | Wing length | Mass | Wing length |
| 0[a] | 0.464* | 0.050* | 0.509* | 0.179* |
| 2 | 0.163* | 0.083* | 0.722* | 0.449* |
| 4 | 0.110* | 0.062* | 0.387* | 0.090* |
| 6 | 0.139* | 0.032 | 0.444* | 0.120 |
| 8 | 0.154* | 0.050* | 0.382* | 0.400* |
| 10 | 0.068* | 0.042 | 0.021 | 0.266* |

* $P < 0.05$.

[a] Regression equations of mass ($M$, in g) on egg size ($E$, in cc) for age 0 days: Masked Booby, $M = 0.820E - 5.081$ (significance of slope, $F_{1,88} = 76.2, P < 0.001$; of intercept, $t = 0.78, P > 0.05$); Blue-footed Booby, $M = 0.583E - 9.867$ (significance of slope, $F_{1,31} = 32.2, P < 0.001$; of intercept, $t = 1.60, P > 0.05$).

the hatching-mass ratio on hatching interval and egg-volume ratio showed that both independent variables accounted for significant variation in the hatching-mass ratio in Masked Boobies (hatching asynchrony, $t = 5.54, P < 0.001$; volume ratio, $t = 2.91, P = 0.005$), but not in Blue-footed Boobies (volume ratio did not enter model at $P = 0.15$). Thus, the egg-volume ratio appears to favor A-chicks in Masked Boobies, but favors neither chick consistently in Blue-footed Boobies. However, the egg-volume ratio had no significant effect on an indicator of competitive advantage (i.e. number of days Masked Booby A-chicks required to kill their siblings). In a multiple regression of days to brood reduction on hatching asynchrony and egg-volume ratio, the effect of egg-volume ratio was not significant ($t = 0.18, P = 0.86$).

Rather than indicating adaptive differences in the brood-reduction system, the differences between the species in the egg-volume ratio may be proximate phenotypic effects of differences in food supply. Blue-footed Boobies lay larger clutches, raise larger broods, and make shorter foraging trips than do Masked Boobies (Nelson 1978, Anderson and Ricklefs 1987), all consistent with greater food availability for female Blue-footed Boobies than for female Masked Boobies when allocating physiological resources for second eggs. If so, Blue-footed Booby B-eggs should vary less in size across years than those of Masked Boobies; data from 1984 through 1986 support this prediction. The volume of A-eggs in two-egg Masked Booby clutches did not vary significantly across the three years ($F_{2,168} = 1.66, P > 0.05$), while that of B-eggs did ($F_{2,168} = 8.36, P < 0.001$); neither A-/nor B-egg volumes of Blue-footed Boobies were heterogeneous across years (A-eggs, $F_{2,71} = 0.46, P > 0.05$; B-eggs, $F_{2,71} = 0.33, P > 0.05$). As a result, the egg-volume ratio was heterogeneous across years for Masked Boobies ($F_{2,168} = 6.40, P < 0.01$), but not for Blue-footed Boobies ($F_{2,71} = 0.16, P > 0.05$).

*Nest-shape differences.*—Both species nest on the ground, but while Masked Boobies simply clear debris from a nest site and deposit eggs there, Blue-footed Booby eggs and small chicks are contained within a bowl-shaped depression (Nelson 1978:plate 12). On two occasions during nest watches, I observed Blue-footed Booby A-chicks pushing their hatchling siblings from under the brooding parent in the manner of Masked Booby chicks (unpubl. data). However,

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TABLE 2. Mean egg volumes and egg-volume ratios (±SD) for two-egg booby clutches. Mean egg-volume ratios differ from ratio of mean A-volume to mean B-volume because A- and B-egg volumes covary (Anderson 1989c; see Welsh et al. 1988).

| Year | n | Volume (cc) | | Egg-volume ratio |
| | | A-egg | B-egg | |
|------|---|---------|---------|-----------------|
| | | Masked Booby | | |
| 1984 | 66 | 70.68 ± 5.44 | 65.64 ± 5.43 | 1.079 ± 0.058 |
| 1985 | 46 | 68.82 ± 4.53 | 62.16 ± 6.12 | 1.113 ± 0.089 |
| 1986 | 59 | 69.80 ± 5.78 | 61.40 ± 6.92 | 1.148 ± 0.156 |
| | | Blue-footed Booby | | |
| 1984 | 45 | 59.24 ± 5.30 | 57.42 ± 5.03 | 1.034 ± 0.072 |
| 1985 | 18 | 60.15 ± 5.70 | 58.48 ± 5.55 | 1.030 ± 0.030 |
| 1986 | 11 | 60.84 ± 5.83 | 58.29 ± 5.25 | 1.045 ± 0.068 |

in both cases the Blue-footed Booby B-chicks rolled down the steep sides of the nest into the shade of the parent when released by the A-chick, suggesting that parents could use nest shape to influence the outcome of the A-chick's efforts. Specifically, obligately siblicidal Masked Boobies will facilitate early siblicide by using a flat nest, and facultatively siblicidal Blue-footed Boobies will suppress early siblicide with a steep-sided, bowl-shaped nest.

A two-way ANOVA of $\Gamma$, the maximum steepness of the nest scrape, with species and nest-age class (10- to 13-day intervals since laying of first egg; see Fig. 2) as main effects, showed that Blue-footed Booby nests were significantly steeper than were Masked Booby nests (species effect, $F_{1,132} = 64.1$, $P < 0.001$). This difference
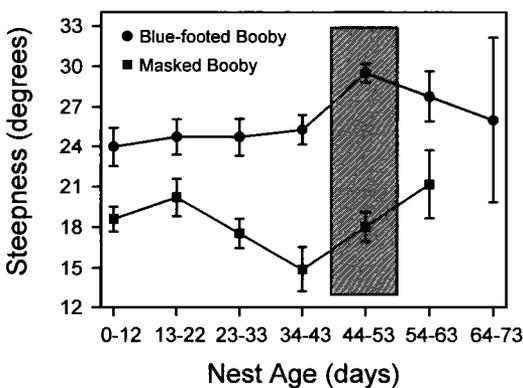


Fig. 2. Maximum steepness ($\Gamma$) of Masked and Blue-footed booby nests in relation to time since laying of nest's first egg. Eggs hatched at approximately 44 days. Period of Masked Booby siblicide indicated by shading. Data presented as $\bar{x} \pm$ SE.

was most marked preceding and during the 44- to 53-day age class, when Masked Booby siblicide occurs. Blue-footed Booby chicks in this age class were in wider (radius of 175 vs. 127 mm, $t = 4.36$, df = 14, $P < 0.001$) and deeper (44.7 vs. 21.6 mm, $t = 4.71$, df = 14, $P < 0.001$) nest scrapes than were Masked Booby chicks. This is a meaningful difference to a highly altricial (i.e. feeble) nestling with a body length of 15 mm. A chick attempting to evict its sibling from a Blue-footed Booby nest would face a slope 64% steeper and 38% longer than would a chick in a Masked Booby nest.

In comparison to ground-nesting seabird species that are not obligately siblicidal, Masked Boobies had the flattest nests measured (Table 3), further suggesting a link between nest steepness and the brood-reduction system. Masked Booby parents used existing slight depressions as nest-scrape locations, but Blue-footed Booby parents actively excavated and regulated bowl depth. This point was demonstrated experimentally with eight Blue-footed Booby nests at the egg stage by filling them with dirt and packing the fill. The nests' dimensions were measured three times in the subsequent 48.5 h, and the measurements compared with the original nest dimensions. Nest width was not consistently affected by the manipulation. Nest depth was initially significantly different from the original depth, but returned gradually to the original dimensions within 48.5 h (Table 4).

When $\Gamma$ values were classed by time since the eggs were laid (Fig. 2), variation across age class was significant in Blue-footed Boobies ($F_{6,90} = 3.19$, $P < 0.01$), but not in Masked Boobies ($F_{5,44} = 1.41$, $P > 0.05$). Blue-footed Booby parents were remarkably attentive to the shape of their

TABLE 3. Γ-values ($\bar{x} \pm$ SD with $n$ in parentheses) for ground-nesting seabirds.

| Species | Nesting-cycle stage | Γ (degrees) | Source[a] |
|---|---|---|---|
| **Single-egg, single-chick species** | | | |
| Red-tailed Tropicbird (*Phaethon rubricauda*) | Egg | 32.4 ± 6.0 (18) | 1 |
| | Hatchling | 29.2 ± 3.9 (8) | 1 |
| **Multiple-chick species** | | | |
| Cape Cormorant (*Phalacrocorax capensis*) | Egg | 54.6 ± 10.6 (16) | 2 |
| Crowned Cormorant (*P. coronatus*) | Egg | 64.9 ± 3.6 (7) | 2 |
| Bank Cormorant (*P. neglectus*) | Egg | 63.6 (21) | 3 |
| | Hatchling | 65.6 (21) | 3 |
| Blue-footed Booby | Egg | 24.8 ± 4.6 (51) | 4 |
| | Hatchling | 29.5 ± 3.7 (48) | 4 |
| **Obligately siblicidal species** | | | |
| Masked Booby | Egg | 17.8 ± 3.4 (27) | 4 |
| | Hatchling | 18.0 ± 4.5 (17) | 4 |

[a] Source: (1) D. J. Anderson, unpublished data from Johnston Atoll, Central Pacific Ocean; (2) R. E. Ricklefs, unpublished data from Malgas Island, South Africa; (3) Cooper 1986; (4) this study.

nests. Parents restored their experimentally filled nests to a steepness that closely matched the original steepness (Spearman rank correlation, $r = 0.93$, $n = 6$, $P < 0.01$). In nonexperimental nests, Γ increased immediately prior to hatching, with peak values and lowest variability during the critical period in which siblicide occurs in Masked Booby nests (i.e. during the first 10 days after hatching), but not in Blue-footed Booby nests (Fig. 2). I did not attempt to observe the behavior used to form nest bowls. However, the soil in Blue-footed Booby nesting areas is dry and fine-grained, and easily can be excavated with a tool resembling a booby's foot (K. Huyvaert unpubl. data).

Blue-footed Booby nest steepness is greatest at precisely the time that steepness is required for suppression of hatchling siblicide, and is less steep and deep at other times (Fig. 2). I identified a possible cost to maintenance of a deep nest: hypothermia of hatchlings during heavy rains, when Blue-footed Booby hatch-

lings were partially submerged in a pool of water, and Masked Booby hatchlings were completely dry. In 1986, rain fell on 25 of the total days that I was present on the island (Fig. 3). The total accumulation during 17 of those days was less than 10 mm; little mortality occurred of Blue-footed Booby nestlings of 20 days or less (three deaths). On the remaining eight days, 10 to 43 mm were recorded daily, filling Blue-footed Booby nests with water and causing hatchling body temperatures to drop (pers. obs.). On these eight days, 17 Blue-footed Booby nestlings of 20 days or less died (Fig. 3). Causes of mortality other than hypothermia (e.g. predation and starvation) could be ruled out in most of these 17 cases. Nestlings older than 20 days were not affected by heavy rainfall: only 2 of 24 (0.08) deaths in this age group occurred on days with at least 10 mm of rain, compared with 17 of 32 (0.53) deaths in the 0- to 20-day age group.

I compared the mortality rates of nestlings

TABLE 4. Nest shapes (width and length, $\bar{x} \pm$ SD; mm) following experimental filling of Blue-footed Booby nest scrapes. An egg hatched in two nests before the second measurement; these nests not measured after hatching occurred.

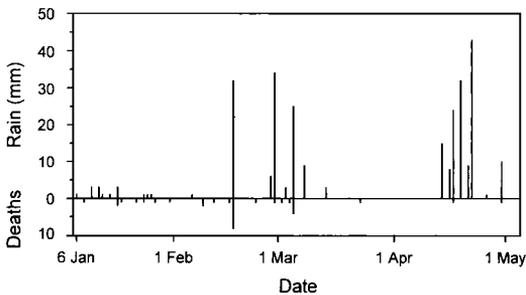| Hours after filling of nest | $n$ | Width (mm) | Paired comparison | | Depth (mm) | Paired comparison | |
|---|---|---|---|---|---|---|---|
| | | | $t$ | $P$ | | $t$ | $P$ |
| Original | 8 | 298.8 ± 41.9 | — | — | 29.0 ± 5.42 | — | — |
| 4.5 | 8 | 284.5 ± 36.2 | 1.35 | >0.20 | 15.6 ± 6.55 | 6.30 | <0.001 |
| 24.5 | 6 | 270.0 ± 27.2 | 2.91 | <0.05 | 24.2 ± 6.68 | 2.36 | 0.07 |
| 48.5 | 6 | 293.3 ± 28.8 | 1.38 | >0.10 | 31.8 ± 5.91 | 0.06 | >0.90 |

Fig. 3. Rainfall (above) and Blue-footed booby nestling mortality for birds in 0- to 20-day age class in 1986.

from the 0- to 20-day age group that were present on a given day as a function of rainfall on that day. I used data from the period of 6 January through 7 March only, because after 7 March the number of nestlings in this age group never exceeded three, reducing the precision of the mortality-rate estimate. During the 6 January to 7 March period, the number present averaged $11.4 \pm 5.8$ nestlings per day. A higher proportion of these nestlings present died on days with at least 10 mm of rain than died on days with less than 10 mm (mean arc-sin transformed daily proportions were 0.39 and 0.03, respectively; $t = 7.44$, df = 68, $P < 0.001$). This test is conservative with respect to the conclusion that rainfall and mortality are linked, given that three of the four deaths that occurred after 7 March happened on days with at least 10 mm of rain.

Masked Boobies in their flatter nests remained dry during rainfalls, and none of the 17 deaths of A-chicks in the 0- to 20-day posthatching age group occurred on days with at least 10 mm of rainfall. Blue-footed Booby parents that had nests characteristic of Masked Boobies might have similarly low hatchling mortality, but the limited variation in Blue-footed Booby nest shape around the time of hatching (Fig. 2) did not allow that comparison. However, nest shapes of Blue-footed Boobies prior to hatching were consistent with regulation toward flatness: a one-way ANOVA of $\Gamma$ showed significant heterogeneity across nest age classes ($F_{6,90} = 3.19$, $P < 0.01$), and nests were consistently flatter prior to hatching than during and shortly after hatching (Fig. 2). Masked Booby $\Gamma$-values did not show similar heterogeneity ($F_{5,44} = 1.41$, $P = 0.24$). In spite of the relative flatness

prior to hatching, Blue-footed Booby nests were still steeper than Masked Booby nests during the first four nest age classes (Fig. 2; two-way ANOVA, nest age class and species as main effects; species effect $F_{1,70} = 32.52$, $P < 0.001$).

DISCUSSION

My goal was to identify factors that contribute to the differences between Masked and Blue-footed boobies in their brood-reduction systems. I detected no contribution of within-clutch egg-size differences, although interspecific differences in this factor are consistent with a regulatory role. However, a novel factor, nest shape, differs between the two species: Blue-footed Booby nests, like those of other ground-nesting seabirds sampled, have steep sides that impede ejection by hatchling chicks, but Masked Boobies have atypically flat nests, facilitating ejection. Moreover, nest shape is closely regulated by Blue-footed Boobies in a manner that should suppress siblicidal ejection of hatchling offspring.

Comparative studies allow one to test the hypothesis that regulatory mechanisms are adapted to maximize reproductive success. Two studies have approached this issue by comparing hatching asynchronies of obligately and facultatively siblicidal eagles (Edwards and Collopy 1983) and boobies (Anderson 1989a). Both found that parents of obligately siblicidal species hatched eggs at longer intervals (thus establishing more biased competitive hierarchies) than did parents of facultatively siblicidal species. Because obligately siblicidal offspring prevent parents from raising more than one chick, even with short hatching intervals (Anderson 1989a), these data are consistent with a hypothesis of adaptive adjustment of hatching asynchrony that cuts losses early. However, they are also consistent with a proximate-level hypothesis that the food limitation that restricts brood size also restricts the rate of egg formation.

The contrasting nest shapes of parent Masked and Blue-footed boobies offer clearer evidence of an adapted regulatory mechanism that has responded evolutionarily to both costs and benefits. The difference is not explained by the most likely alternative hypotheses. For example, thermal considerations suggest that nestlings in the hotter environment should have a flatter nest to increase exposure to air flow. The study site is equatorial, and both species nest in ther-

mally stressful situations, but the pattern is the opposite of that predicted: Masked Boobies have significantly cooler, windier nest sites than do Blue-footed Boobies (Anderson et al. unpubl. manuscript). Another alternative hypothesis involves the nature of the substrate: possibly a bowl-shaped nest is optimal for both species, but perhaps the soil in Masked Booby colonies does not permit formation of a bowl. Masked and Blue-footed boobies do show nesting segregation into different areas (Duffy 1984), but the ease of digging in the two areas is not substantially different. A similar degree of digging effort yields a hole approximately 20% shallower in Masked Booby areas than in Blue-footed Booby areas (Anderson et al. unpubl. manuscript), but the difference in nest depths that I found in this study approached 100% at the time of hatching.

In conclusion, hatching asynchrony clearly influences the speed of obligate siblicide in Masked Boobies, but cannot provide a proximate-level explanation for the difference in social systems between Masked and Blue-footed booby hatchlings (Anderson 1989a). Hatchlings of both species are capable of siblicidal behavior, but Blue-footed Booby *A*-chicks face a significant obstacle to ejecting siblings in the wider, steeper nest bowl than Masked Booby chicks face. Experimental modifications of nest shape in these two species that do not disturb parents and especially during periods of heavy rain would complement this comparative approach to costs and benefits of nest steepness. Manipulation of the "arena" in which sibling aggression occurs has not been suggested previously as a mechanism for regulating the outcome of the interactions; this appears to have a proximate effect on brood size in these two species.

## ACKNOWLEDGMENTS

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APPENDIX

This proof, in conjunction with Figure 4, shows that the angle FAD (which approximates the steepness of a nest) can be calculated when the lengths of lines AD and DE are known from field measurements. The steps in the proof are as follows: (1) Angle AED = tan⁻¹ (AD/DE). (2) Angle ACE = 180° − 2(AED) because triangle ACE is isoceles triangle. (3) Angle ACB is complement of angle ACD, and angle CAD is complement of angle FAD. (4) Angle ACB equals angle CAD because lines BC and AD parallel, so angle ACD = angle FAD = angle ACE. (5) Thus, from 1 and 2, angle FAD = 180° − 2[tan⁻¹ (AD/DE)].
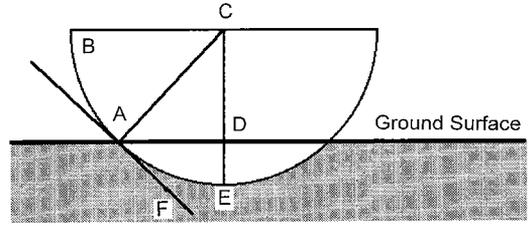


Fig. 4.   Idealized vertical cross-section of a booby nest. Only shaded region exists at actual nest site. Angles and shapes described in Appendix. Semicircular shape represents assumption that nest-bowl surfaces conform to that of a section of a sphere.