The Adaptive Significance of Siblicide in Nazca Boobies

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Introduction

Galapagos is home to an incredible collection of seabirds, many found nowhere else in the world. One such bird, the elegant and slightly comical Nazca booby, is one of three booby species found in the archipelago. It is the booby you are second most likely to see when visiting, and there are between 25,000 and 50,000 breeding pairs living only on Espanola, San Cristobal, and Genovesa. Nazca boobies feed primarily on fish and plunge dive offshore from heights of up to 328 feet, gracefully collapsing their wings at the last moment before they enter the water (Kricher 2006: 108). Unlike its red and blue-footed cousins, the Nazca booby’s feet are not vibrant, but rather a plain olive. Whatever beauty their feet may lack is more than made up for by pristine white body feathers, and wings and tail rimmed with pure black plumage.

As elegant as the adult Nazca booby is, as a chick it exhibits some rather unsightly behavior—murder. Without fail, Nazca boobies are obligately siblicidal; their normal two-egg clutch is always reduced to one by either unsuccessful hatching of one egg, or siblicidal aggression of the older chick (Anderson 1990b: 346). This strange behavior is not unique to the Nazca booby species, blue-footed
booby chicks sometimes exhibit siblicide, but the condition does bring up some interesting questions. In particular, why has siblicide evolved in this species, and given that it has, why do Nazca boobies still lay two eggs? Fortunately, the Nazca booby has been the central object of study for David Anderson for more than two decades, and there is data available on investigations into the many hypotheses regarding siblicide in this species. A few are unsupported, some seem fairly likely, but there is still no concrete evidence, and it is unlikely we can ever know the exact evolutionary history of siblicide.

The evolution of siblicide

A Nazca booby nest consists of a relatively flat circular area cleared of debris marked by a simple guano ring, Nazcas do not dig out a slight bowl-shaped depression like blue-footed boobies do, nor do they use any sort of extra nesting material to protect or insulate the eggs (Anderson 1995: 864). Nazca boobies lay their first egg on their bare ground nest and immediately start incubating, laying the usual second egg four to nine days later (Clifford 2002: 275). This laying asynchrony is directly proportional to the hatching asynchrony of the eggs, which is “among the longest of all birds...resulting [in] size and developmental disparities” (Clifford 2002: 374). By the time the second chick is born, the first-born chick or A chick is significantly larger than the second-born because it has had several days of feeding and growing (Kricher 2006: 310). The size difference that results from hatching asynchrony is a death sentence for the B chick because it makes it much easier for the A chick to expel it by “grasping in its beak the siblings neck, appendage, or skin and extending its neck to thrust the B-chick across the nest scrape.” The graph below clearly shows the sharp decline in days it takes for brood reduction as the hatching asynchrony increases. Once a chick is out of the nest scrape the parent boobies will not acknowledge it, and it will die quickly either by predation, starvation, or temperature change (Anderson 1995: 861-862).
The behavior of Nazca booby chicks is considered siblicide because it “makes a direct and significant contribution to the immediate death of a sibling nest mate,” but it is important to distinguish it from the form of siblicide present in another Galapagos booby species. In blue-footed booby broods, chicks are siblicidal only if there is not enough food, and this is called facultative siblicide because it is “conditional on the perpetrator’s immediate ecological and physiological situation.” By contrast, Nazca booby siblicide is obligate, meaning that it does not depend on ecological conditions, but is “persistent [and] unconditional” (Anderson 1990b: 337-338).

The immediate question that follows is how such a barbaric, and seemingly detrimental, behavior evolved in this avian species. The siblicidal nestling loses inclusive fitness when it kills the B chick because it shares on average half of its genes with its sibling, so there must be some gain in direct fitness otherwise this behavior would not have evolved. One hypothesis which would seem to nicely explain this behavior is recurrent food scarcity, because the growing A chick would have unhindered access to parental resources once it killed its nest mate, and would have a survival and reproductive advantage by developing on schedule. David Anderson and his research team tested this hypothesis by experimentally doubling Nazca booby broods to see whether or not the parents could actually provide enough food to feed two growing chicks. Their procedure was to take eggs from different nests that
were laid at the same time and put them in the same nest to see if the parents would be able to feed both, and these were compared to control groups of single-egg nests. It was necessary to experimentally double the broods because that way there would be little to no hatching asynchrony, and consequently the chicks would be less likely to succeed in expelling one another from the nest scrape. The results were that parents with two chicks in the nest increased their foraging efforts and were able to keep two chicks fed. At peak food intake, doubled broods got only 41% more food than singletons, which led them to be slightly smaller with age, but still a relatively healthy size (Anderson 1990a: 2073).

Even though the doubled broods had chicks that were a pretty healthy size, they did have a higher mortality rate than single chicks, meaning that even though there is not currently enough food scarcity to *necessitate* siblicide, at some point in the past there may have been a strong enough pressure to evolve obligate siblicide (Anderson 1990a: 2074, 2077). It is easiest to think of the evolution of obligate siblicide as the invasion of an allele whose phenotype is siblicidal behavior. During a time of strong selection pressure to exclude nest mates from the limited food source, a chick born with the allele for siblicidal behavior (as a result of genetic mutation) would be at an advantage, and this allele could quickly invade a population (Anderson 1990a: 2078). Once the populations is “fixed on the
siblicidal strategy...the nonsiblicidal strategy could not invade [because] most broods containing a nonsiblicidal A chick should also contain a siblicidal B chick,” therefore even though there is apparently no longer any strong selection pressure for siblicide it persists because the nonsiblicidal allele cannot reinvade (Anderson 1990a: 2079).

One study done during the siblicidal age range of Nazca boobies (zero to seven days) aimed to find out how three hormones generally related to aggression and development in other animals related to siblicide in Nazca boobies. The three hormones studied were picked because testosterone is “often involved in aggressive behavior of vertebrate animals,” and progesterone and corticosterone “may be involved in body mass regulations...[which] typically influences the outcome of aggressive competition among nesting birds” (Tarlow 2001: 14-15). The researchers predicted that testosterone was responsible for the direct regulation of siblicidal behavior and that progesterone and corticosterone provided the developmental advantage (specifically a rapid increase in body mass relative to length) that enabled the success of the siblicidal behavior. What they found was that young chicks “showed endocrine changes consistent with the hypothesis that steroid hormones may be involved in the regulation of fatal social interactions.” The levels of CORT and P show a preliminary correlation to the increase in the A chick's body mass when it has a second ‘challenge’ egg it share the nest with. An important part of a larger chart is shown here that illustrates the overall levels of testosterone for young chicks. As predicted A is highest, but the one above B is a sample that was taken during an aggressive siblicidal act (the only observed case of a B chick ejecting an A chick successfully) and indicates that “the secretion of [testosterone] may be a direct, but short duration, response to a social challenge (Tarlow 2001: 15-19). Overall, hormonal correlates need to be researched further to determine their exact role in siblicide of Nazca boobies.
The persistence of two-egg clutches

It is clear from the current state of siblicide in Nazca boobies and the application of games theory described above that Nazca boobies are highly unlikely to ever reverse to nonsiblicidal behavior. When this fact settles in, it stirs up another very important question: why do Nazca boobies still lay two-egg clutches even though they only ever have one chick? The first possible explanation is that they might actually be in the middle of evolution toward one-egg clutches, as it seems that parents would have a higher fitness by not wasting energy on a second egg that will not result in a fledgling. This was tested by observing how many clutches are naturally one or two eggs. The percentage fluctuates from year to year, in the chart below three consecutive years are shown and the last shows more one-egg than two-egg clutches.

However, 1986 was an El Nino year, meaning that food for the Nazca booby was probably scarce. To test the hypothesis that food scarcity causes the unusually high amount of one-egg clutches, mothers were supplemented food to see if food intake affected clutch size. The results were that 92% of supplemented females laid two eggs, and only 70% of control females laid two eggs, suggesting that the optimum clutch size for Nazca boobies remains two, despite the evolution of siblicide (Clifford 2002: 278).

If two-egg clutches continue to be favored, then there must be some reproductive advantage to having two eggs despite that the extra cost of the second egg does not result in a second surviving chick. There are three hypotheses here explored that aim to explain what this

<table>
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<tr>
<th>YEAR</th>
<th>1 egg</th>
<th>2 eggs</th>
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<tr>
<td>1984</td>
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<td>67</td>
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<td>1985</td>
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<td>71</td>
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<td>TOTAL</td>
<td>177</td>
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*Anderson 1990b*
advantage might be, the Icebox Benefit Hypothesis, the Progeny Choice Benefit Hypothesis, and the Insurance-Egg Hypothesis. The Icebox Benefit Hypothesis assumes that the B chick is essentially a store of fresh food for the rest of the family and that families with this extra food have a reproductive advantage over families without a B chick during times of food shortage (Boag 2005: 381). There has never been an observed case of within-family cannibalism in Nazca boobies, and even B chicks that die within the nest scrape are simply left until they are “eventually ground into the nest substrate.” B chicks that are ejected from the nest usually die of predation by other animals such as Sally Lightfoot crabs, starvation, and in only one observed case, cannibalism by a neighboring unrelated adult Nazca booby (Boag 2005: 385-386). Because of the lack of any evidence that supports within-family cannibalism at any time, the Icebox Benefit Hypothesis is pretty certainly not the explanation for the persistence of two-egg clutches.

The Progeny Choice Benefit Hypothesis assumes that the B chick will live long enough to compete with the A chick for the permanent spot in the brood, and also assumes that sometimes the B chick will win. This competition would result in the strongest chick surviving, meaning that the parents have increased reproductive fitness by raising the chick that is most likely to continue the genetic line (Boag 2005: 381). However, the chart below shows that the average cohabitation time is very short, in fact, “brood reduction occurred within 10 days of the [B] chick's hatching in all nests except one,” and during this ten day period the B chick is so small and frail that it could hardly be any real challenge to the A chick. Only one case out of 1,901 really supports the Progeny Choice Benefit Hypothesis, so it is also not likely as the explanation for continuing two-egg clutches (Boag 2005: 387).
The third hypothesis investigated here is the Insurance-Egg Hypothesis, which assumes that the reproductive fitness cost of laying the B egg is less than its in insurance value in the event that the A chick should either fail to hatch or die before the B chick hatches (Evolution 1990b: 337). Also, the Insurance Egg Hypothesis “predicts that two-egg clutches should always yeied higher reproductive success than do one-egg clutches” (Clifford 2001: 341). Researchers recorded the hatching and fledging successes of natural one and two-egg clutches to see if there was indeed a reproductive advantage to laying a second egg. They found that there was an insignificant difference in hatching success of individual eggs between the clutch sizes, but that the two egg clutches had a “higher probability of hatching at least one chick” (Anderson 1990b: 343). This higher probability of hatching at least one chick from a two-egg clutch shows a reproductive advantage, but for the Insurance Egg Hypothesis, the cost of laying the egg must be less than this gain. The cost of laying an egg has not been determined in Nazca boobies, but for the related red-footed booby it has been determined to be an average daily investment of
1%-2.4% of the booby’s daily energy expenditure (Anderson 1990b: 344). The fact that B eggs “contributed the surviving hatchling in 19.2% of...two-egg clutches” shows that there is a significant advantage to two eggs that outweighs the parental investment of laying the egg (it is important to note that the B egg hatchling survivors did not kill the A chick, they survived after either the A chick failed to hatch or died before the B chick hatched) (Anderson 1990b: 342). The chart below illustrates that not only was the probability of fledging higher in natural two-egg clutches, but was also higher in experimentally doubled clutches than reduced clutches, consistent with the Insurance Egg Hypothesis’ prediction that two eggs should always be advantageous (Clifford 2001: 340).

<table>
<thead>
<tr>
<th>Probabilities</th>
<th>Fledging</th>
<th>C1</th>
<th>C2</th>
<th>Reduced</th>
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<td>0.77</td>
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<td>Late lay period</td>
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<td>0.47</td>
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Clifford 2001

Conclusions

We will probably never be able to determine exactly what caused obligate siblicide to evolve in Nazca boobies, but the most promising explanation seems to be that some past selection pressure, probably food scarcity, caused a siblicidal allele to invade the population that cannot revert even now that the selection pressure is gone and parents are able to forage for two chicks. Through the investigation of several hypotheses, it appears most likely that the Nazca boobies optimum clutch size continues to be two despite the effects of siblicide because the B egg provides a significant insurance value against the premature failure of the A egg or
chick. Some further research is needed both to understand the mechanisms that control siblicide and why the B egg is needed as insurance. Hormonal correlates have been preliminarily investigated, but it is still unclear why boobies have such a low hatching success that they need two eggs. Nazca boobies “hatch 51%-61% of their eggs, whereas single-egg [obligately siblicidal] species all hatch at least 85% of their eggs.” This is one possible area of further research because “the majority of unhatched eggs contain no visible embryo, indicating that embryos died shortly after fertilization or were never fertilized”; either the ground temperature of the nest scrape is above the lethal temperature for avian embryos, or Nazca booby infertility is “exceptionally high,” either of which would be fascinating areas for further research (Anderson 1990b: 343-345).
Bibliography

*All pictures taken by Annikka Frostad-Thomas except the one marked with a blue star in the corner, which is from a now broken website which can only be accessed at


Boag, Peter T, and David J Anderson. "Contributions of marginal offspring to reproductive success of Nazca booby (Sula granti) parents: tests of multiple hypotheses." Wilson

