

Clutch size variation in the Nazca booby: a test of the egg quality hypothesis

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In obligately siblicidal bird species, aggressive behavior by a dominant chick results in a fixed brood size of one, yet these species usually show clutch size variation between individuals. Simmons proposed that variation in clutch size in obligately siblicidal species is related to a trade-off between egg quality and egg quantity: some individuals produce a single highly hatchable egg, while others produce two small, lower quality eggs. We tested the egg quality hypothesis as an explanation for observed clutch size variation in the Nazca booby (*Sula granti*), an obligately siblicidal seabird. We tested the assumption that egg volume is positively correlated with hatchability and the prediction that eggs from one-egg clutches are larger than eggs from two-egg clutches. We did not find a positive relationship between egg volume and hatchability in this species. Eggs from two-egg clutches were either equivalent in volume or larger than eggs from one-egg clutches. Thus, the egg quality hypothesis was rejected as an explanation for clutch size variation in the Nazca booby. Instead, two-egg clutches appear to be favored because of the insurance value of the second-laid egg, while one-egg clutches result from food limitation. *Key words*: clutch size variation, egg quality hypothesis, Nazca booby, obligate siblicide, *Sula granti*. [*Behav Ecol* 13:274–279 (2002)]

Obligately siblicidal birds present a particularly interesting case of clutch size variation because, despite a fixed brood size of one, some individuals produce multiple-egg clutches. Theoretical (Forbes, 1990; Forbes and Lamey, 1996) and empirical evidence (Anderson, 1990; Cash and Evans, 1986; Clifford and Anderson, 2001a) indicates that second eggs act as insurance, providing a chick for the parents to raise when the first egg fails to hatch or when the first chick dies shortly after hatching. Because two-egg clutches confer a reproductive advantage on females producing them, selection should act against the production of one-egg clutches. Some individuals of obligately siblicidal species nonetheless produce one-egg clutches. In one of these cases, experimental evidence from the Nazca booby (*Sula granti*) suggests that food limitation during egg formation explains the existence of one-egg clutches (Clifford and Anderson, 2001b), despite selection favoring production of an insurance egg (Clifford and Anderson, 2001a).

Simmons (1997) suggested an alternative, adaptive explanation for clutch size variation within obligately siblicidal taxa: one- and two-egg clutches represent alternative strategies, with some individuals laying one large, high-quality egg and others laying two small, lower quality eggs. In this view, large, single eggs have high hatchability and produce more robust chicks, and two-egg clutches trade off size-related disadvantages with the insurance value of the second egg. This egg quality hypothesis can be considered a mixed evolutionarily stable strategy (Maynard Smith, 1982) in which different clutch sizes achieve the same payoff in fitness through trade-offs between egg size and egg quality (Nur, 1986). The egg quality hypothesis (EQH) predicts that eggs from one-egg clutches are larger than eggs from two-egg clutches, based on the assumption that large eggs have higher hatching success and/or higher offspring viability than small eggs. Here we tested both the assumption and the prediction of the EQH with data from

the Nazca booby. We also addressed the application of the EQH to clutch size variation between species of the genus *Sula*.

The Nazca boobies of the Galápagos have traditionally been considered masked boobies (*Sula dactylatra granti*), but recent analyses of morphological and breeding data (Pitman and Jehl, 1998) and of mitochondrial DNA differentiation (Friesen et al., submitted) support elevation of the Galápagos and nearby populations to species status. In this article, we follow the nomenclature of Pitman and Jehl (1998) and the American Ornithologists' Union (2000) and refer to these birds as Nazca boobies.

METHODS

We conducted this fieldwork in the Galápagos Islands, Ecuador, at Punta Cevallos, Isla Española (1°20' S, 89°40' W; see Anderson and Ricklefs, 1987) from 1984 to 1986 and from 1992 to 2000. The Nazca booby breeds annually, producing a clutch of one or two eggs. The proportion of birds that produce two-egg clutches ("c2") and one-egg clutches ("c1") differs between years (Anderson, 1990). When both eggs from a c2 clutch hatch, the first hatched chick ("A-chick") ejects the second-hatched chick ("B-chick") from the nest, and the B-chick dies from exposure or predation (or, rarely, the A-chick dies before siblicide; Anderson, 1993). In 15 years of field work at this site, we have never seen an unmanipulated pair of Nazca boobies fledge two chicks in a single reproductive attempt (Anderson, unpublished data; Clifford and Anderson, personal observations).

The egg-laying period on Española is from November to February (Nelson, 1978). We arrived during the egg-laying period each year, although from 1984 to 1986 we arrived late in the egg-laying period (January) and from 1992 to 1999 we arrived in November or late October. On arrival at the Nazca booby colony, we searched a designated area (the study area) for nests that already contained eggs and marked each of these nests with flagging tape. Nazca boobies incubate continuously, and their nests are located along the coastline on the ground, which is generally barren of vegetation. Therefore, nests with eggs are conspicuous and easily located. We did not include these nests in our analyses (unless otherwise noted)

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because a nest containing a single egg on our arrival may have resulted from the loss of an egg from a c2 clutch, and therefore clutch size could not be assigned to single-egg clutches with confidence. After marking all existing nests, we searched the study area daily for new clutches. When we found a newly initiated clutch, we marked the nest with flagging tape and then marked the first-laid egg with a small "A" with a pencil or a nontoxic marker. If a second egg was subsequently laid, we marked it "B." If an egg was laid in a nest and disappeared, and then a new egg was laid in the same nest within 10 days of the first egg being laid, we considered the two eggs to be part of the same two-egg clutch because Nazca booby laying asynchrony is 4–9 days (Anderson, 1993). We continued to monitor clutches daily until we ascertained the fate of all eggs in the clutch. In 1983 and 1984, a few nests still contained eggs being incubated when we left the colony; these were not included in our analyses. We measured the length (L) and breadth (B) of eggs to the nearest 0.1 mm using Vernier calipers and calculated egg volume as $0.00051(LB^2) + 1.22$ (modified from Anderson, 1993).

We used logistic regression to test the assumption implicit in the EQH that large eggs have a higher probability of successfully hatching than small eggs. We analyzed each year separately because Nazca boobies tend to return to their nest sites year after year (Nelson, 1978), and combining data across years would have resulted in non-independence of some data points. Because this analysis did not require us to know the clutch size associated with an egg, we included eggs from nests that were present when we arrived at the colony. After analyzing the volume of all eggs laid in the study area, we repeated the analysis for c1 and c2 clutches separately, using data from A-eggs in c2 clutches to avoid the potential confounding effects of laying order.

By performing the same statistical test for each year, we increased the probability of falsely rejecting a null hypothesis. We used the false discovery rate procedure (Benjamini and Hochberg, 1995), which controls the expected fraction of null hypotheses that are mistakenly rejected, to appropriately adjust observed p values for this problem. The procedure ranks the n comparisons in order of decreasing p values and compares p values to a critical significance level, beginning with the largest p value. The critical significance level for each comparison, d_i , is calculated by dividing the specific comparison i by the total number of comparisons n and then multiplying by the false discovery rate (the expected proportion of null hypotheses mistakenly rejected). For example, the fifth comparison (the comparison with the fifth largest p value) of six total comparisons, given a false discovery rate of 0.05, has a d_i of 0.042 ($= 5/6 \times 0.05$). If the achieved significance level is $< d_i$ for a given comparison, then the null hypothesis is rejected for that comparison and for all subsequent comparisons (Benjamini and Hochberg, 1995; Curran-Everett, 2000).

Hatching success may be affected by factors associated with the female or nest site, rather than egg size. To eliminate such factors, we did a within-female analysis by examining c2 clutches in which only one of the two eggs hatched. We determined how frequently the larger of the two eggs hatched and compared this frequency to an expected frequency of 0.50 (if probability of hatching is independent of volume, then half of the hatchlings in this pool should come from the larger egg) using a goodness-of-fit test. We included each female in the analysis only once; when a female met the criteria for inclusion in the analysis in multiple years, we randomly chose data from one of the years. Nests that were already present when we arrived at the colony were included in this analysis because when two eggs are present in a nest, they generally belong to the same clutch, although occasionally a foreign egg rolls into a nest and is incubated along with the

natural egg(s) (Clifford and Anderson, personal observations).

Regression analyses showed that A-egg volume was not related to clutch initiation date in any year (all p values $> .05$). Therefore, clutch initiation date could be ignored as a factor explaining egg volume, and we used t tests to test the prediction that c1 eggs were larger than c2 A-eggs within each year, using the false discovery rate procedure to adjust p values.

Simmons (1997) envisioned a trade-off of egg quality and clutch size, mediated by variation in egg size. Such a trade-off might still exist even if egg size does not mediate it. To test the hypothesis that egg hatchability and clutch size show negative covariance, as predicted by the trade-off hypothesis, we calculated the proportion of c1 and c2 A-eggs that hatched each year and tested for differences using a Yates corrected chi-square. To eliminate hatching failure due to parental quality and not egg quality per se, we only used eggs that had the opportunity to hatch (i.e., did not disappear or fail before the full incubation period was complete.) We used only data from 1985 and 1992–1997 because other years had too few cases of one clutch size.

RESULTS

Test of assumption: is egg volume correlated with hatchability?

Logistic regression revealed no consistent relationship between egg volume and probability of hatching for the 11 breeding seasons analyzed. A significantly positive relationship existed between egg volume and probability of hatching in 1994, a significantly negative relationship existed in 1983, and no relationship existed in the remaining 9 years (Table 1). These analyses included eggs that failed before the incubation period was complete. Sources of egg failure such as predation after abandonment by parents or accidental breakage during territorial disputes may not reflect intrinsic hatchability of eggs and may confound results. Therefore, we repeated these analyses, eliminating cases in which eggs failed before 49 days of incubation (the longest observed incubation period for Nazca boobies; Anderson, 1993). No significant relationship existed between egg volume and probability of hatching for 10 of 11 years, but a significantly negative relationship existed in 1983 (Table 1).

We separated egg volume data by clutch size to determine if a within-clutch-size relationship between egg volume and probability of hatching was obscured by combining eggs from different clutch sizes. Because we arrived late in the egg-laying period in 1984 and 1985, we were unable to assign clutch sizes to most clutches with certainty in these years. Therefore we excluded these 2 years from the analysis because of their small sample sizes (1984: $n = 0$; 1985: $n = 2$). For c1 clutches and c2 clutches, no significant relationship existed between egg volume and probability of hatching for any year, regardless of whether all clutches were included or only clutches in which eggs persisted for the entire incubation period (Table 2).

Within-female analysis of c2 clutches in which only one egg hatched showed that the larger of the two eggs within a clutch hatched in 50/95 (0.53) cases. This proportion did not differ significantly from the 0.50 expected due to chance alone ($G = 0.26$, $df = 1$, $p = .61$). In an attempt to control for parental quality, we eliminated clutches that lost eggs before the incubation period had ended from the data set and repeated the analysis. The larger of the two eggs hatched in 12/26 (0.462) cases, which was not significantly different from the 0.50 expectation ($G = 0.15$, $df = 1$, $p = .69$).

Simmons (1997) focused on egg size as the indicator of egg quality in framing the EQH. Other characteristics of eggs

Table 1
The relationship (rel; +, positive relationship; -, negative relationship) between egg volume and hatching success as determined by logistic regression

Com- parison	All eggs					Fully incubated eggs ^a				
	Year	Rel	<i>p</i>	<i>d_i</i>	<i>n</i>	Year	Rel	<i>p</i>	<i>d_i</i>	<i>n</i>
# 11	1985	+	.797	0.050	210					
# 10	1996	+	.757	0.045	551	1984	-	.791	0.050	62
# 9	1984	-	.654	0.041	102	1997	-	.695	0.045	249
# 8	1992	-	.643	0.036	197	1985	+	.763	0.040	93
# 7	1998	+	.225	0.032	205	1995	+	.613	0.035	564
# 6	1995	+	.169	0.027	747	1998	+	.578	0.030	116
# 5	1993	+	.158	0.023	451	1992	-	.447	0.025	145
# 4	1999	+	.152	0.018	115	1996	-	.318	0.020	362
# 3	1997	+	.095	0.014	590	1994	+	.218	0.015	619
# 2	1994	+	.008	0.009	839	1993	+	.090	0.010	303
# 1	1983	-	<.001	0.005	102	1983	-	0.003	0.005	85

Years ranked by *p* value (see text). Significant results appear in bold.

^aFully incubated eggs are those that persisted in the nest for the entire incubation period (49 days).

might also influence quality, causing higher hatchability of c1 eggs than of c2 eggs. However, in 1994, a significantly greater proportion of c2 A-eggs than c1 eggs hatched. In all other years we detected no significant difference in hatching success (Table 3).

Test of prediction: are eggs from one-egg clutches larger than eggs from two-egg clutches?

Overall mean egg volume of A-eggs from two-egg clutches laid in 1985 and 1992–1999 was 68.46 cm³, and for B-eggs it was 63.83 cm³. Single eggs from one-egg clutches had a mean egg volume of 66.89 cm³. A-eggs from two-egg clutches were significantly larger than A-eggs from one-egg clutches in 4 of 9 years (Table 4). In the remaining 5 years, no significant difference existed in egg volume between C1 and C2 clutches.

Using the same procedure that we used to compare A-eggs from two-egg clutches to single eggs from one-egg clutches, we compared A-eggs from two-egg clutches to B-eggs from two-egg clutches and found that B-eggs were significantly smaller than A-eggs in 8 of 9 years after controlling for multiple comparisons. Again, using the same procedure, we found

that B-eggs from two-egg clutches were significantly smaller than single eggs from one-egg clutches, after comparing for multiple comparisons, in 9 of 9 years.

DISCUSSION

Egg volume and hatchability in the Nazca booby

Our data revealed no consistent relationship between egg volume and probability of hatching in Nazca boobies. Between-clutch analyses generally produced no significant relationship between these two variables, indicating that small and large eggs were equally likely to hatch. We found that large eggs had a significantly higher probability of hatching than small eggs did in 1994, but this relationship disappeared when we eliminated eggs that failed during the incubation period. This may have resulted from low-quality females tending to lay small eggs, which they subsequently either abandoned or lost during the incubation period. Thus, parental quality and not egg size may explain the cases of association between size and hatchability. A number of studies that have controlled for effects of parental quality have concluded that egg size does not

Table 2
Results from logistic regression analyses indicating whether a significant relationship exists between egg volume and probability of hatching

c1 clutches				c2 clutches, A-eggs									
All eggs				Fully incubated eggs ^{a,b}			All eggs ^b			Fully incubated eggs ^c			
Year	<i>p</i>	<i>d_i</i>	<i>n</i>	Year	<i>p</i>	<i>n</i>	Year	<i>p</i>	<i>n</i>	Year	<i>p</i>	<i>d_i</i>	<i>n</i>
1985	.597	0.050	34	1993	.924	27	1997	.710	168	1994	.966	0.050	107
1992	.450	0.044	14	1995	.655	46	1995	.611	262	1992	.887	0.044	21
1996	.381	0.039	74	1985	.457	12	1996	.595	145	1998	.700	0.034	3
1998	.357	0.033	31	1996	.373	31	1993	.420	69	1993	.675	0.031	48
1994	.266	0.028	46	1994	.307	20	1992	.418	28	1985	.475	0.025	8
1997	.246	0.022	62	1992	.300	12	1994	.388	159	1997	.418	0.019	61
1993	.118	0.017	49	1997	.273	12	1999	.382	17	1995	.315	0.013	211
1999	.096	0.011	53				1998	.303	7	1996	.016	0.006	97
1995	.037	0.006	74	1985	.26		15						

Years ranked by *p* value (see text).

^aNo logistic regression could be performed for 1998 (*n* = 6) or 1999 (*n* = 7) when all eggs hatched.

^bNo *d_i* is included for these groups of analyses because no comparison had a *p* value < .05.

^cNo logistic regression could be performed for 1999 (*n* = 7) when all eggs hatched.

Table 3
Proportion of eggs that hatched in a given year, excluding eggs that failed during the incubation period (sample sizes in parentheses)

Comparison	c1	c2 A-eggs	χ^2	p	d_i
# 7: 1992	0.83 (12)	0.76 (21)	0.00	.967	0.050
# 6: 1995	0.87 (46)	0.86 (211)	0.01	.911	0.043
# 5: 1985	0.58 (12)	0.63 (8)	0.08	.780	0.036
# 4: 1997	0.67 (12)	0.80 (61)	0.44	.507	0.029
# 3: 1996	0.74 (31)	0.88 (97)	2.28	.131	0.021
# 2: 1993	0.70 (27)	0.88 (48)	2.31	.129	0.014
# 1: 1994	0.45 (20)	0.80 (107)	9.39	.002	0.007

Years ranked by p value (see text). Significant differences appear in bold.

influence hatching success (Bolton, 1991; Meathrel et al., 1993; Reid and Boersma, 1990; Smith et al., 1995; but see Amundsen et al., 1996). Ignoring clutch size and laying sequence, a significant negative relationship existed between egg volume and hatchability in 1983, indicating that small eggs had a higher probability of hatching than large eggs. This relationship persisted after removing eggs that failed before the incubation period ended. The overall pattern in our data indicated that larger eggs did not have a higher probability of hatching, and thus the assumption of the EQH is not supported.

By eliminating eggs that failed during the incubation period from our analyses, we hoped to partially control for parental quality. Parents that abandoned or otherwise lost eggs during this period may have been among the poorest quality parents, but a range of parental qualities probably still existed for parents of clutches that persisted until hatching. Another way to control the confounding effect of variable parental quality is to compare the probability of hatching for eggs within a clutch. Our intraclutch comparisons showed that when only one of the two eggs in a two-egg clutch hatched, the probability of the larger egg hatching did not depart significantly from the 0.50 expected under a null model. This suggests that large-egg volume, independent of parental quality, does not result in increased hatchability of Nazca booby eggs. However, our strictest test of this relationship had a sample size of 26, with a power of only 0.17 to detect a departure from 0.50 of 0.10. We should therefore be cautious in our interpretation of these results. Potti and Merino (1996) found no intraclutch difference in volume between eggs that hatched and eggs that failed in pied flycatchers (*Ficedula hypoleuca*). Other studies of intraclutch egg-size variation have found an unclear relationship between egg volume and hatchability, with laying sequence being more important than egg size (Robertson and Cooke, 1993; Williams et al., 1993).

In a broader version of the assumption, unspecified characteristics of costly c1 eggs might increase hatchling production to the same degree as cheaper insurance eggs do in c2 clutches, in the quality/number trade-off envisioned by Simmons (1997). We found no such trend: hatchability was unrelated to clutch size in all years except one, in which c2 eggs showed higher hatchability than c1 eggs did.

In summary, our data do not support the assumption of the EQH; interclutch comparisons showed no clear increase in hatchability of large eggs compared to small eggs, and intraclutch comparisons did not indicate an increase in hatchability with egg size. C1 eggs did not show higher hatching success than c2 eggs did. In contrast, some studies have shown an increase in hatching success for large eggs compared to small

Table 4
Mean volumes of A-eggs from one- and two-egg clutches

Comparison	c1	c2	t	df	p	d_i
# 9: 1999	66.71	66.88	0.11	63	.916	0.050
# 8: 1992	66.39	66.12	0.17	39	.868	0.044
# 7: 1985	68.22	68.82	0.37	50	.715	0.039
# 6: 1996	67.72	68.70	1.21	203	.228	0.033
# 5: 1998	67.55	69.42	1.28	71	.206	0.028
# 4: 1994	65.69	68.37	2.35	185	.020	0.022
# 3: 1995	66.63	68.51	2.75	333	.006	0.017
# 2: 1997	68.12	70.66	2.92	229	.004	0.011
# 1: 1993	65.00	68.65	3.20	100	.002	0.006

Years ranked by p value (see text). Years in which mean egg volume differed significantly appear in bold.

eggs (e.g., Potti and Merino, 1996; Simmons, 1997; Weidinger, 1996; Wiebe and Bortolotti, 1995). However, these studies did not control for variation in parental quality, so it is unclear whether increases in hatching success are due to high-quality parents that lay large eggs, or to egg volume per se.

The EQH and clutch size variation in the Nazca booby

Our data did not support the prediction of the EQH that eggs from c1 clutches are larger than eggs from c2 clutches. In contrast, the overall pattern was for size of c2 A-eggs to equal or exceed that of c1 eggs. If increases in egg volume had conferred an advantage in terms of hatchability, then c2 A-eggs would be of higher quality than c1 eggs, and one- and two-egg clutches would not be equivalent strategies for producing a hatchling, as posited by the EQH.

We did not find a clear relationship between hatching success and egg volume, which could be taken to indicate that egg volume and egg quality are independent of each other. If this is true, the EQH might still explain clutch size variation in the Nazca booby under the assumption that c2 eggs are low quality in some other respect, whereas c1 eggs are high quality. However, our data indicated that c2 A-eggs either had equal or significantly greater hatching success than did c1 eggs. This indicates that c2 A-eggs were equivalent in intrinsic hatchability to c1 eggs in some years and superior in others.

We have focused on egg hatchability as the relevant component of fitness, but Simmons (1997) identified variation in offspring viability as another potential consequence of variation in egg quality. In his study of clutch size in eagles, Simmons used egg size to indicate egg quality, and numerous studies have indeed demonstrated positive covariance between egg size and posthatching growth and/or survival (reviewed by Williams, 1994; for Nazca boobies, see Anderson and Ricklefs, 1995). Although this covariance may result in part from variation in general parental quality covarying with both egg size and chick performance, hand-rearing studies (e.g., Anderson et al., 1997) and cross-fostering experiments (Magrath, 1992; Nisbet, 1978) that remove parental quality effects on growth also identify a positive effect of egg size itself. In Nazca boobies, large egg size might affect posthatching components of fitness that we did not examine. We cannot test this assumption nonexperimentally in Nazca boobies because parental quality (success raising hatched chicks) covaries with clutch size (Clifford and Anderson, 2001a). However, c2 A-eggs were larger than c1 eggs in 8 of the 9 years of our study, so the quality/number trade-off of the EQH (at least as mediated by egg size) cannot be supported. Elsewhere we showed that supplemental feeding resulted in the production

of c2 clutches by 92% of fed Nazca boobies compared to only 70% of controls (Clifford and Anderson, 2001b); this suggests that the explanation for most c1 Nazca booby clutches lies in food limitation.

The EQH and interspecific clutch size variation in the genus *Sula*

Simmons (1997) proposed that the EQH can explain clutch size differences between obligately siblicidal species and closely related species that lay a single egg. He cites differences in absolute egg volume (not relative egg volume) and hatching success between booby species (*Sula* sp.) in support of the EQH. However, when corrected for body size, *Sula* eggs are approximately equal in size (log egg volume/log female mass = 0.55 – 0.58, excluding the Abbott's booby; Anderson, 1990). The similarity of relative egg sizes of *Sula* species suggests that they should be considered equal in quality under the assumption of the EQH, yet hatching success ranges from 51% to 98% (Anderson, 1990). Rather than reflecting an effect of egg volume, the observed range in hatching success may be related to the species' breeding ecology (Anderson, 1990). The EQH and breeding ecology hypotheses both invoke differences in hatching success to explain interspecific differences in clutch size, but the root causal factor differs: under the former, egg quality–clutch size covariance results in selection for different clutch sizes, while under the latter, differences in breeding ecology result in selection for different clutch sizes.

The EQH as a potential explanation for clutch size variation in other species

Although we did not find support for the EQH in the Nazca booby, the EQH may explain clutch size variation in other species. Few studies have found a relationship between hatching success and egg volume (see above); however, several lines of reasoning suggest that such a relationship could exist. Large eggs have a higher surface-to-volume ratio than small eggs and are therefore less susceptible to fluctuations in temperature that may damage or kill the developing embryo. Furthermore, because of the surface-to-volume relationship, large eggs lose proportionately less water through evaporation (Drent, 1975). Both temperature (Drent, 1975; Webb, 1987) and water loss (Drent, 1975) are important determinants of hatching success.

In the absence of a relationship between hatching success and egg volume, the EQH may nevertheless be supported if large eggs confer some other advantage. A number of studies have shown that large eggs produce larger hatchlings, hatchlings that grow faster, and/or hatchlings that survive better than do small eggs (review in Williams, 1994; see also Amundsen et al., 1996; Blomqvist et al., 1997; Perrins, 1996; Smith et al., 1995). Therefore, a trade-off between egg number and egg quality may indeed exist in these species.

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