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Evolution of single-chick broods in the Swallow-tailed Gull *Creagrus furcatus*

ANA AGREDA¹† & DAVID J. ANDERSON²*

¹Department of Biology, Catholic University of Ecuador, Quito, Ecuador

²Department of Biology, Wake Forest University, Winston-Salem NC 27109–7325, USA

Swallow-tailed Gulls lay single-egg clutches, and so raise single-chick broods. As they are pelagic seabirds, this small brood size is expected to relate to proximate food limitation owing to infrequent food deliveries. However, a previous brood doubling experiment detected an 82% increase in fledging success from experimentally doubled broods compared to controls. We repeated the brood doubling experiment, and found that none of 50 enlarged broods produced more than one independent offspring. Control and experimental parents produced fledglings of similar body size, which also had indistinguishable rates of fledging and subsequent survival and reproduction. A variety of parameters estimating survival and breeding costs of reproduction showed no treatment effect. Since two-chick broods yield dramatically higher fledging rates at some times, apparently without excess costs of reproduction, selection on brood size appears to favour a two-chick brood. However, selection may not favour a two-egg clutch if egg production is very costly. Additionally, our estimates of reproductive success do not incorporate the performance of experimental and control offspring as adults, which could differ, since growth of chicks differed slightly by treatment.

INTRODUCTION

Pelagic seabirds are noted for their low reproductive rates, raising single-chick broods with long growth periods. These single-chick broods have long been viewed as products of proximate ecological constraint: their pelagic foraging biology limits how frequently food can be delivered to nest-bound young, and only one slowly growing chick can be supported at a time (Ashmole 1971, Lack 1968, Nelson 1977, Ricklefs 1983). Tests of this 'food limitation hypothesis' have monitored the growth and survival of nestlings in singleton broods and experimentally doubled broods, and have generally concluded that pelagic seabird parents can, in fact, raise two chicks to fledging (reviewed by Ydenberg & Bertram 1989, Anderson 1990). The fledging success of doubled broods was higher than that of controls in most studies (e.g. Atlantic Puffin *Fratercula arctica*: Corkhill

1973), and in only a minority of studies was equal to (e.g. Cape Gannet *Sula capensis*: Navarro 1991) or less than that of controls (e.g. Laysan Albatross *Phoebastria immutabilis*: Rice & Kenyon 1962). Moreover, time budget data indicate that some single-chick seabirds have substantial unused foraging capacity during chick-rearing (Anderson & Ricklefs 1992). Thus, the proximate food limitation hypothesis can be rejected as a general explanation of evolution of brood size in pelagic seabirds, but little work has been done to test other hypotheses. Of particular interest are reproductive costs incurred during current reproduction that may influence future performance, such that the long-term reproductive rate of control parents would exceed that of experimental parents even when short-term fledging rates indicate the reverse.

Life history theory is rooted in the premise that unavoidable tradeoffs link demographic traits. One such tradeoff is that between current reproductive effort and future survival and reproduction, assumed to be negatively correlated (Roff 1992, Stearns 1992). Among pelagic seabirds, a cost of reproduction driving the tradeoff could result from increased mortality risk when foraging to provision current young, drawing

*Corresponding author.

Email: da@wfu.edu

†Present address: Department of Biology, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, MO 63121–4499, USA.

on stored resources during current reproduction to the detriment of long-term physiological condition, and other factors. These costs of reproduction are distinct from indirect costs, which are paid by the parents in terms of 'grandchildren' if control offspring survive and reproduce better than experimentals do. Neither cost of reproduction has been investigated in relation to pelagic seabird brood size using adequate sample sizes (e.g. Anderson (1990) found neither subsequent survival nor reproduction effects, but might have done so with larger samples).

One of the most dramatic results from brood enlargement experiments with pelagic seabirds came from Harris's (1970) study of Swallow-tailed Gulls *Creagrus furcatus* in the Galápagos Islands, in which experimental broods that were given a second hatchling on the day of their own egg's hatching fledged 82% more young (1.02 offspring/brood) than did controls (0.56 offspring/brood). Eight of 30 experimental families (0.266) fledged both chicks (Harris 1970). He also followed banded parents after fledging and detected no excess mortality in experimental parents and concluded that parents could 'rear two young with no apparent difficulty' (Harris 1970). Experimental and control offspring had similar nestling periods and body sizes at fledging, so no obvious indirect cost of reproduction was indicated. These results suggested that selection favoured the evolution of two-chick broods, yet clutch size in this species is one (Harris 1970, D.J. Anderson pers. obs.). Brood size may be limited by egg production, but the fact that incubating adults have two brood patches suggests a recent evolutionary history of two-egg clutches.

To evaluate further the possibility that brood size has not responded to selection, we repeated Harris's experiment 30 years later, also in the Galápagos at a site 70 km from Harris's study site. Our objectives were to compare the nestling growth, fledging brood sizes, and post-breeding survival and reproduction of parents from natural and enlarged broods, to give a multiyear perspective on selection on brood size.

STUDY AREA AND METHODS

The fieldwork was conducted in the mixed seabird colony, including 800 pairs of Swallow-tailed Gulls, at Punta Cevallos, Isla Española, Galápagos Islands, Ecuador (1°23'S, 89°37'W). Anderson and Ricklefs (1987) give details of the study site. During March–June 1996, 310 nests with eggs were marked with flagging tape and monitored daily, noting laying dates and nest failure. Length (L) and breadth (B) of

each egg was measured (except for one experimental egg) with Vernier calipers, and each egg was individually marked with a non-toxic Sharpie pen. Egg volumes were calculated using the equation $V = L \times B^2 \times \pi/6$ (Preston 1974). Same-aged eggs were randomly designated as control, experimental or donor. On the day of hatching for an experimental nest, a pipped donor egg was introduced, and a previously designated control nest with a pipping egg was identified as the experimental nest's age-matched control. Hatching asynchronies in experimental nests were 0 days (42 cases), 1 day (seven cases) or 2 days (one case). Aside from this manipulation, control and experimental nests were treated identically. Donor nests were not monitored after removal of the egg. We assembled 50 experimental/control nest pairs in this manner.

Almost all control (98/100) and experimental (98/100) adults were marked with a numbered aluminium band on the right leg. All nests were monitored daily after hatching, and measurements of chicks (wing, ulna, culmen and mass) were taken every 5 days between hatching and fledging (the date of the first flight away from the nest). Nests were also monitored during the 2–3 weeks after fledging during which offspring are still present. Chicks were not individually marked, so donor and original chicks could not be differentiated. At age 50 days chicks received a numbered aluminium band on their right leg. When emaciated chicks died after an extended period of poor growth, we recorded starvation as the cause of death.

To monitor post-experiment survival and breeding, the nesting colony was checked daily from December 1996 until May 1997 for the presence of banded birds. Since successful pairs breed at 9-month intervals, and unsuccessful pairs at a shorter interval (Harris 1970), this period was the appropriate time to attempt recaptures during the subsequent breeding attempt. Leg band numbers of birds present were read with binoculars or by capturing the bird and reading it in the hand. Nests of banded birds were monitored daily to record laying date, hatching date and presence/absence of the chick. Egg measurements were taken as in the previous year. After hatching, chicks were measured every 5 days. A final visit to the colony was made in March 1999 and all banded birds present were recaptured and their band numbers recorded.

Data analysis was performed with Statistica (Statsoft Inc. 1999), and statistical tests were considered significant at the $P = 0.05$ level. Repeated measures ANOVAS

of nestling growth included a single categorical variable (control/experimental) and nestling body size measurements at 5-day intervals. When contingency table cells had zero counts, 0.5 was added to all cells. When testing for differences between treatment groups, we employed the false discovery rate procedure (Benjamini & Hochberg 1995) to adjust P values for multiple comparisons when appropriate. The procedure requires comparisons to be ordered by decreasing P values, and then compared to the $\alpha_{\text{crit}i}$ denoted d_i , beginning with the largest P value. 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 (α) of 0.05, has a d_i of 0.042 ($= 5/6 \times 0.05$). If the achieved significance level is less than the d_i for a given comparison, then the null hypothesis is rejected for that comparison, and all remaining comparisons (Benjamini & Hochberg 1995, Curran-Everett 2000).

RESULTS

Period of brood enlargement

Mean egg volumes of control (72.35 mL, $sd = \pm 5.34$) and experimental (71.95 mL, $sd = \pm 5.97$) parents did not differ in 1996, the year of brood enlargement ($t = 0.34$, $df = 97$, $P = 0.73$). Hatchling measurements on the day of hatching did not differ by treatment (MANOVA Wilk's Lambda = 0.874, $df_1 = 4$, $df_2 = 62$, $P = 0.08$; culmen: control mean = 17.1 mm [$sd = 0.9$], experimental mean = 17.2 mm [$sd = 0.7$]; ulna: control mean = 26.1 mm [$sd = 1.6$], experimental mean = 26.0 mm [$sd = 1.4$]; wing chord: control mean = 23.4 mm [$sd = 1.1$], experimental mean = 22.7 mm [$sd = 1.3$]; mass: control mean = 54.5 g [$sd = 6.2$], experimental mean = 54.7 g [$sd = 5.0$]).

One experimental brood produced two fledglings (volant young), but one of these died 3 days after fledging. We considered this brood as fledging a single young in all analyses. With this proviso, no experimental broods produced two fledglings. The 50 control broods produced 38 fledglings (0.76 of nests were successful), and the 50 experimental broods produced 36 fledglings (0.72 successful; $G = 0.21$, $df = 1$, $P = 0.65$). However, per capita survival of control chicks to fledging (0.76) was significantly higher than that of experimentals (0.36; $G = 22.12$,

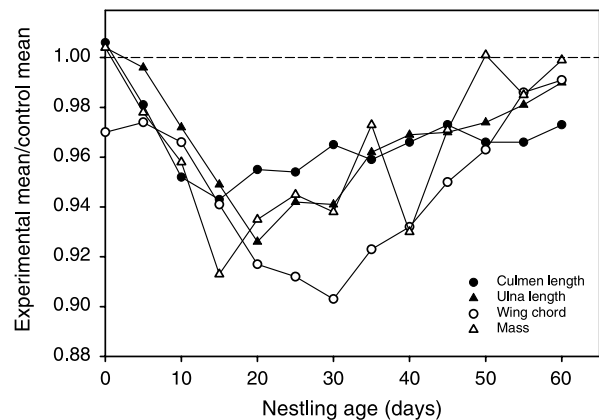


Figure 1. Mean values of four morphological characters of experimental chicks that survived to fledging, in relation to the means of same-aged control chicks that survived to fledging.

$df = 1$, $P < 0.0001$). Starvation was a more important cause of mortality among experimental chicks than among controls, accounting for 47 of 64 (0.73) deaths among experimentals but only 4 of 12 (0.33) deaths among controls ($G = 6.91$, $df = 1$, $P < 0.01$). A variety of other causes, including predation, accidents and unusually high tides, accounted for the small number of remaining deaths in both groups. All mortality in controls, and 89% in experimentals, occurred by day 40; median age at death of control (20 days) and experimental (20 days) offspring did not differ significantly (Mann-Whitney $U = 361.5$, $Z = 0.24$, $N_1 = 12$, $N_2 = 63$, $P = 0.81$). Average age at fledging for control (70.66 days, $sd = \pm 8.23$) and experimental offspring (70.41 days, $sd = \pm 6.28$) did not differ significantly ($t = 0.15$, $df = 73$, $P = 0.88$).

For chicks surviving to fledging, the growth of experimentals lagged behind that of controls for two of the four morphological measures (Fig. 1). In all four repeated measures ANOVAs, the repeated measure term (age) was highly significant ($P < 10^{-6}$) and the treatment \times age term was not significant ($P > 0.10$). Applying the false discovery correction for multiple comparisons, the treatment term was significant for culmen length ($F_{1,71} = 8.68$, $P = 0.004$, $\alpha_{\text{crit}} = 0.013$) and marginally significant for ulna length ($F_{1,71} = 5.97$, $P = 0.017$, $\alpha_{\text{crit}} = 0.017$), but not for mass ($F_{1,71} = 2.80$, $P = 0.10$, $\alpha_{\text{crit}} = 0.025$) or wing chord ($F_{1,68} = 2.61$, $P = 0.11$, $\alpha_{\text{crit}} = 0.05$).

Period after brood enlargement

The probability of resighting after the experimental breeding period was similar for banded control (84/

98 = 0.86) and experimental parents (83/98 = 0.85; $G = 0.00$, $df = 1$, $P = 1.00$). Among birds that were resighted, we could determine whether pairs remained intact across sequential breeding attempts for 45 control pairs and 44 experimental pairs; this probability of mate retention was similar (control: 0.36; experimental: 0.33; $G = 0.03$, $df = 1$, $P = 0.88$). For pairs that remained intact, we calculated the number of days between egg-laying during the experimental breeding attempt and their subsequent egg-laying. The mean duration of this period was similar for controls (274 days, $sd = \pm 28.2$) and experimentals (284 days, $sd = \pm 25.5$; $t = 1.44$, $df = 58$, $P = 0.15$).

Of the birds resighted after the experimental period, similar proportions of control (78/84 = 0.93) and experimental birds (78/83 = 0.94) initiated new clutches during our monitoring ($G = 0.08$, $df = 1$, $P = 0.78$). Mean egg volumes of controls (71.77, $sd = \pm 4.25$) and experimentals (72.79, $sd = \pm 5.57$) did not differ ($t = 0.77$, $df = 55$, $P = 0.44$). Hatching success of controls (50/78 = 0.64) and experimentals (55/78 = 0.71) did not differ ($G = 0.72$, $df = 1$, $P = 0.39$), nor did fledging success from hatched eggs (controls: 21/50 = 0.42; experimentals: 21/55 = 0.38; $G = 0.16$, $df = 1$, $P = 0.69$). Of birds that failed to hatch their first egg, re-nesting occurred at similar frequencies among controls (14/28 = 0.50) and experimentals (12/23 = 0.52; $G = 0.02$, $df = 1$, $P = 0.88$). Growth of young fledged by pairs including at least one control parent did not differ from that of pairs including at least one experimental parent (treatment terms of repeated measures ANOVA, culmen length: $F_{1,40} = 0.25$, $P = 0.62$; ulna length: $F_{1,40} = 0.21$, $P = 0.65$; wing chord: $F_{1,40} = 2.02$, $P = 0.16$; mass: $F_{1,40} = 0.77$, $P = 0.39$).

Short-term and long-term enlargements

Of experimental parents that had two chicks for 10 days or less during the brood enlargement period ('short-term enlargements'), 22/53 (0.42) raised a chick to fledging age in the subsequent breeding cycle. The corresponding data for parents that had two chicks for at least 30 days ('long-term enlargements') was 6/24 (0.25) and for controls was 37/98 (0.38; G -test of all three groups, $G = 2.05$, $df = 2$, $P = 0.38$), a non-significant difference.

Resighting probabilities in the next breeding cycle were similar for parents with short-term enlargements (45/53 = 0.85) and parents with long-term enlargements (19/24 = 0.79; Yate's Corrected

$\chi^2 = 0.39$, $df = 1$, $P = 0.53$). Of the parents that were resighted in the next breeding cycle, the probability of initiating a clutch in that cycle was also similar for parents with short-term enlargements (42/45 = 0.93) and parents with long-term enlargements (18/19 = 0.95; Yate's Corrected $\chi^2 = 0.05$, $df = 1$, $P = 0.83$). Among parents that laid an egg in the next breeding cycle, parents with short-term enlargements were no more likely to fledge a chick in that cycle (22/42 = 0.52) than were parents with long-term enlargements (6/18 = 0.33; Yate's Corrected $\chi^2 = 1.87$, $df = 1$, $P = 0.18$). The same comparison between control parents (21/78 = 0.27 laid eggs produced a fledgling) and parents with long-term enlargements also revealed no difference (Yate's Corrected $\chi^2 = 0.30$, $df = 1$, $P = 0.59$).

Resightings in March 1999 revealed no difference between control (33/98 = 0.34) and experimental birds (31/97 = 0.32; Yate's Corrected $\chi^2 = 0.01$, $df = 1$, $P = 0.91$). Experimental parents that had short-term enlargements were resighted at a similar frequency (20/53 = 0.38) to that of parents with long-term enlargements (11/24 = 0.46; Yate's Corrected $\chi^2 = 0.18$, $df = 1$, $P = 0.67$). None of the offspring from the experimental breeding season was seen in either the subsequent breeding cycle or in March 1999.

Overall reproductive success in relation to brood size

Across the two breeding cycles, 16 control parents produced no fledglings, 52 produced one and 30 produced two (1.14 fledglings/banded parent), while 17 experimental parents produced no fledglings, 57 produced one and 24 produced two (1.07 fledglings/banded parent; Mann-Whitney $U = 4522$, $Z = 0.71$, $N_1 = 98$, $N_2 = 98$, $P = 0.48$). No difference existed among short-term experimentals, long-term experimentals and controls (Kruskal-Wallis $H = 0.26$, $df = 2$, $P = 0.88$).

DISCUSSION

Our results differed markedly from those of Harris (1970): we detected no reproductive advantage of parents with enlarged broods. No experimental parents raised two chicks to independence, owing to starvation among experimental chicks, indicating food limitation on brood size. Most starvation mortality occurred before 40 days of age; growth of surviving experimental chicks showed some evidence

of depressed growth during this period, further indicating food limitation. This food limitation capped the brood size at independence at one offspring, and control and experimental broods yielded similar short-term reproductive rates.

Considering long-term treatment effects, the similar mean body sizes at fledging and identical mean fledging ages of experimental and control offspring gave no indication that experimentals will perform differently from controls as subadults and adults. A marginal difference may eventually favour controls, since surviving controls had slightly larger body sizes through most of their growth than experimentals did, and fledging body size and post-independence performance are positively correlated in some birds (Perrins *et al.* 1973, Garnett 1981). While we found no reproductive advantage for experimental parents, we detected no notable additional costs either. A variety of survival and reproductive parameters measured after the experiment showed no evidence of reproductive costs borne by experimental but not control parents. In the simplest interpretation of our results, parents delivered enough food for a single chick, early starvation of experimentals brought chick food demand into line with this limited supply, and experimental parents made no costly effort to increase food delivery, as would be indicated by impaired future performance.

To apply this interpretation to Harris's (1970) results, one must only assume that food availability was high enough during Harris's experiment for experimental parents to support two chicks without a costly increase in reproductive effort (since Harris also detected no excess cost of reproduction associated with treatment). According to this view, parental investment (*sensu* Trivers 1972) in provisioning

does not exceed some ceiling that typically can supply a single chick, but in years of high food availability more than one chick may be raised. This assumption of a low-effort ceiling on provisioning is supported by experimental results from some species (e.g. Leach's Storm Petrel *Oceanodroma leucorhoa*: Ricklefs 1987) but not others (e.g. Nazca Booby *Sula granti*: Anderson 1990). Harris's experiment was conducted 30 years before ours, and on an island 70 km away, so food availability may well have been substantially different. Comparison of breeding parameters from Harris (1970) and our study offers some support for this idea (Table 1): the masses of breeders and fledglings and the interval between clutches all indicate more favourable conditions during Harris's experiment. The difference in fledging success between the two studies does not contradict the idea, since starvation was a minor cause of the higher mortality in Harris's study.

Given the data from these two studies, selection on clutch and brood size should favour the evolution of two-chick broods, since Harris's results show that they sometimes yield a dramatically higher reproductive rate than do single chick broods, without attendant costs. However, additional selective influences that we have not considered may outweigh the reproductive advantage that Harris detected, with net selection favouring a single egg. Neither Harris (1970) nor our study estimated the cost of laying and incubating a second egg, although Harris (1970) found that hatching success per egg of experimental two-egg clutches (0.52) did not differ significantly from that of single eggs (0.65). Indirect costs of reproduction via grown offspring, in which brood size influences production of 'grandoffspring', have not been investigated except to estimate offspring

Table 1. Comparison of reproductive parameters of Swallow-tailed Gulls from Harris's (1970) study and our 1996 study. Breeding status (incubation, chick-rearing) was not specified for birds providing mass data in 1970; incubating birds provided mass data in 1996 (Agreda and Anderson, unpubl. data). Asymptotic nestling mass in 1970 estimated from Harris (1970, Fig. 8). If available, standard deviations of means are given in parentheses.

	Harris (1970) singletons	1996 study	
Breeding mass			
males (g)	713 (59)		670.1 (23.3)
females (g)	673 (40)		609.8 (50.3)
		<u>Control</u>	<u>Experimental</u>
Fledglings/brood	0.56	0.76	0.72
Asymptotic nestling mass (g, day 65)	~620	581.8 (66.3)	602.2 (61.3)
For clutches producing a fledgling, days between clutches	244–268	274 (28.2)	284 (25.5)

condition at fledging. Any such costs must be large, though, to outweigh an 82% reproductive advantage accruing in some years (in one of two studies) to parents of two-chick broods.

Alternatively, clutch size may be constrained genetically to a single egg. This argument is more persuasive for taxa within a clade that historically produced single-egg clutches, such as petrels (Warham 1990), and in which clutch size may be phylogenetically constrained. In the case of gulls, only the Swallow-tailed Gull produces single-egg clutches. Moreover, it has two brood patches. The constraint hypothesis could be falsified by supplemental feeding experiments prior to and during the egg formation period. Additional future work should focus on estimates of physiological and demographic costs of egg production, and on repetitions of our brood enlargements to determine how frequently environmental conditions permit fledging of experimental two-chick broods.

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