BREEDING BIOLOGY OF LAUGHING GULLS IN FLORIDA. PART I: NESTING, EGG, AND INCUBATION PARAMETERS

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The Laridae is perhaps the most studied family of marine birds. Although the Laughing Gull (*Larus atricilla*) is an abundant nesting species along the Atlantic Coast of the United States, until the present decade little was known about its breeding biology. The present work continues our earlier study (Dinsmore and Schreiber, 1974). We present here details on colony size, nest density, timing of laying, and hatching and fledging successes as they relate to clutch and egg size. Part II will present data on growth of nestlings, as related to sequence of hatching, egg weight, and clutch size.

STUDY AREA AND METHODS

Our study area was on an unnamed island (designated 49b in Schreiber and Schreiber, 1978) on the west coast of Florida on the Bayway, Boca Ciega Bay, southern Pinellas County. It is a rectangular land fill established about 1960, across a 100-m channel from a housing development, and is further described in Dinsmore and Schreiber (1974) with photographs in Schreiber and Schreiber (1975). On 17 April 1975, we established a 150 × 40-m study area on the mid-south portion of the island and visited it daily, until 100 nests were marked, on 8 May. During the following 15 days we visited the island five times, and during the hatching period from 23 through 31 May we again made daily nest checks. Through June and July we visited the colony every fourth day. We weighed and measured eggs (to the nearest 0.1 g and 0.01 mm) as they were laid using dial calipers and an Ohaus triple beam balance. Chicks were measured (culmen, wing, tarsus) with dial calipers and a 0.5-meter stick as described in Schreiber (1970) and Hailman (1961). At hatching we marked the wings or head of the nest mates with a red (3M brand) permanent felt-tip pen and then banded them at 3–4 days of age with U.S.F.W.S. bands. Just prior to hatching we erected a 50-cm high chicken wire fence with 2.5-cm mesh around nests in three separate regions of the colony; each fence held about eight nests. However, pulli repeatedly attempted to escape from the enclosure, badly damaging their culmen and forehead. Some adults tried to feed chicks through the fence, causing a high death rate from starvation. We removed the fencing and released the pulli on 27 June. Thus we lost data on growth and development and fledging success.

In 1976, the Schreibers visited the colony weekly from mid-March through 24 April. From 25 April through 4 May (10 days) we checked nests twice a day, at approximately 0700 and 1900, each visit lasting one to two hours. During the incubation period we checked nests approxi-

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mately every third day. When hatching began we checked nests daily at 1800 from 21 to 28 May (eight days) and then at approximate three-day intervals through 11 July.

Nests were marked in two separate areas, one in the mid-south portion of the island near the 1975 study area and one to the east. Similar data were collected as in 1975 on egg and pulli size and weight, although we used Pesola spring balances to determine weight. We recorded the stage of nest construction at which a nest received an A egg. Nest construction stages were divided as follows: scrape, bare circular area of ground (often dug out 2–4 cm); scrape+, a few pieces of vegetation in the scrape; medium−, scrape in which ground is almost covered with nest material; medium+, nest material is more than one layer thick; well−, a circular flat pile of nest material but no cup is formed; and well+, nest with well formed nest cup.

Just prior to hatching we enclosed eight nests in the east area and 33 nests in the mid-island area with 40-cm high black roofing paper. Since the birds could not see through this paper, they made no attempt to escape and adults readily fed young inside the enclosure.

We banded 600 young in 1974, 2,389 in 1975, and 1,800 in 1976 in this colony. In 1977, the Schreibers visited the colony on 21 and 29 April and on 12 May, and determined colony size, nest density, clutch size, and stage of breeding cycle. Schreiber and Schreiber (1978) summarized data on timing of the nesting seasons in 1974–1977 for several Laughing Gull colonies throughout Florida.

RESULTS AND DISCUSSION

Colony Size and Nest Density

We do not have precise data on the size of this colony, but we estimated 20–25,000 pairs in 1975, 1976, and 1977, up from the 15,000 pairs estimated in 1972 and 1973. During the winter-spring of 1976 the mainland portion of this colony was graded into a golf course and no nesting occurred on the mainland in that year or in 1977. In previous years no nesting had taken place in the easternmost 300 m of the island but the total island was utilized for nesting in 1976 and 1977.

In 1972, the average distance between nests was 195 cm (Dinsmore and Schreiber, 1974). In 1975, we counted one nest per 6.84 m^2, with an average distance between nests of 103 cm ($n = 67$). In 1976, we counted one nest per 6.06 m^2, with an average distance between nests of 89 cm ($n = 51$). In 1977, we counted one nest per 3.12 m^2. These data for the same area at a similar stage of the nesting cycle indicate that the density and number of nesting pairs in this colony increased in later years, as has the area of the island occupied.

Bongiorno (1970) found a density of about one nest per 32–35 m^2 in Laughing Gulls in New Jersey salt marshes, and Montevecchi (1977) recorded approximately one nest per 0.48 ac in another part of those marshes. Obviously this Laughing Gull colony is much denser.

TABLE 1

Length of incubation period in relation to the stage of nest completion at laying of the first egg in the clutch, 1976.

Incubation period	Stage of nest construction				
	Scrape+	Medium−	Medium+	Well−	Well+
$\bar{x}$	24.9	24.7	24.4	24.3	24.0
(n)	(10)	(7)	(10)	(17)	(10)
SD	0.516	0.488	0.459	0.588	0.158
Range	24–26	24–25	24–25	23.5–25	24–24.5
Significance[1]	AB	CD	A	BD	AC

[1] Each $\bar{x}$ is significantly different (t-test, $P < .05$) from the means having the same letter listed in this row.

Nest Construction

Contrary to what Montevecchi (1976) found, Laughing Gulls in Florida colonies begin laying while the nests are in almost any stage of completion, except as bare scrapes. Perhaps this represents different responses to the substrate and is an example of the plasticity of this behavior in gulls. In Florida some scrapes with only a few pieces of vegetation received eggs and the nest was then completed by the laying of the C egg (Table 1). Most nests received eggs before they were completed. A "complete" nest is one at the final stage of construction; no more material is added and it does not change shape.

Nest size and the amount of material used in the nest varied greatly. It was impossible to document if less well-built nests belonged to younger birds. Most nest material consisted of short (up to 30 cm) pieces of dog fennel (*Baccharus* sp.), the most common plant on the island. No green material was used. The quality of nests did not vary between locations in the colony or with timing of the nesting season. In general nest placement closely follows the details presented by Bongiorno (1970) and Burger and Shisler (1978) for this species in New Jersey, but no flooding has occurred in this colony and thus selection for higher nest sites does not seem to have occurred.

In 1976, 23 of 161 nests (14%) in our study area did not receive eggs. Essentially all of these were built early in the season and no new nests that did not receive eggs were constructed late in the season. Perhaps the birds that built these unused nests later built other nests that were or were not used. Ryder (1976) found that the frequency of unused nests varied seasonally and with the age and experience of the pair in Ring-billed Gulls (*Larus delawarensis*). However, he found a higher percentage of unused nests later in the season, the opposite of our findings for Laughing Gulls.

A comparison of the mean incubation period of eggs laid in nests at different stages of completion shows that incubation periods tend to be shorter in nests that were well completed when the first egg was laid

(Table 1). Eggs laid in well-built nests were heavier ($\bar{x}$ = 1.3 g) than those laid in scrape+ or medium nests, indicating that the longer incubation period in nests incomplete at the laying of the first egg is not due to those nests receiving heavier eggs. Birds in the process of nest construction when the first egg was laid may not begin incubation immediately or the lack of insulation in the unfinished nests may prolong incubation. Perhaps older birds complete their nests before laying and are more efficient incubators.

Daily Cycle of Egg Laying

In 1976, we determined to within 12 hours the time of day when 42 eggs were laid by checking nests at 0700 and 1900 during laying and hatching. These data establish a primary pattern of laying between 1900 and 0700 (27 or 64% of 42 eggs). It may be that most of this laying took place at or close to dawn so our data do not necessarily indicate nocturnal laying. Ytreberg (1960, quoted from Bachrach, 1974) found that the Black-headed Gull (*Larus ridibundus*) and Common Gull (*L. canus*) laid few eggs between 2000 and 0400.

Timing of Egg Laying

In 1976, the first eggs were laid in the colony on 15 April, and the peak of laying was from 26 April to 5 May. In our marked areas 50% of the clutches were completed by 3 May and 75% by 9 May. Laying continued into mid-June, including clutches that were probably relayings, but only 4% of all clutches were laid after 16 May. Timing of the laying was the same in both areas of the colony in 1976, and was essentially the same as in all previous years for which data exist (Dinsmore and Schreiber, 1974; Schreiber and Schreiber, 1978).

In New Jersey marsh colonies of Laughing Gulls (1,100 and 1,300 km to the north of this colony), there is some variability in timing of the first eggs: 18 May 1967 (Bongiorno, 1970), but 9 May in 1976 (Burger and Shisler, 1978). On Monomoy, Massachusetts, Nisbet (1976) showed an advance in date of first laying from 31 May 1972 to 21 May 1975. In New Jersey the peak of nesting occurred around 27 May in the mid-1960's (Bongiorno, 1970) but in 1976 the peak was between 12 and 21 May (Burger and Shisler, 1978).

In all regions studied the peak of laying occurs during an approximate two-week period. The differences in timing between Florida and the northeast United States are the expected differences in timing in more northern vs. southern populations. However, the strict timing of nesting initiation in Florida seems surprising in light of the variability in the northeast. We suspect the different migratory patterns between the two regions may affect the onset of nesting.

Laying Interval

We determined the interval between laying of eggs within the clutch for 38 nests in 1976. Since nests were checked twice daily during this

TABLE 2
Clutch size in Laughing Gulls, 1975 and 1976.

	Clutch size				
	4 Eggs	3 Eggs	2 Eggs	1 Egg	Total
1975					
Number of nests receiving eggs	1	79	14	1	95
Percentage of total nests	1%	83%	15%	1%	100%
Number of eggs laid	4	237	28	1	270
Average clutch size = 2.84					
1976					
Number of nests receiving eggs	0	76	58	4	138
Percentage of total nests	0	55%	42%	3%	100%
Number of eggs laid	0	228	116	4	348
Average clutch size = 2.52					

period, we would expect a ±0.25-day error in these results (see Nisbet and Cohen, 1975). For 3-egg clutches the mean interval between A and B eggs ($\bar{x}$ = 2.03 days ± 0.4, n = 15) was significantly shorter (*t*-test, $P <$ 0.001) than between B and C eggs ($\bar{x}$ = 2.30 ± 0.4, n = 25). The mean interval between A and B eggs in 2-egg clutches ($\bar{x}$ = 2.73 ± 0.8, n = 13) was significantly longer (*t*-test, $P < 0.001$) than either of the above. No differences in laying interval were detected between early and late nesters.

Possibly the production of the last egg of three is a greater energy drain on the female than the production of the first or second, or, merely that it takes the female longer to mobilize the energy reserves for the production of the third egg. The long interval in 2-egg clutches may indicate that some birds cannot produce eggs as efficiently as others.

Few data exist on laying intervals in larids. Nisbet and Cohen (1975) and Parsons (1972) found differences and related these to incubation period and productivity (see discussion below). Nisbet and Cohen (1975) found no significant differences in the laying intervals of A, B, and C eggs or between 2-and 3-egg clutches in Common Terns (*Sterna hirundo*).

Hatching intervals were similar to laying intervals although with only once-a-day nest checks during hatching it is difficult to obtain accurate data for comparison. Parsons (1972) in Herring Gulls, and Nisbet and Cohen (1975) in terns, found shorter hatching intervals than laying intervals and accompanying successively shorter incubation periods for A, B, and C eggs.

We suspect differences may exist in these factors between species and that generalization should be withheld until more species have been studied in detail.

TABLE 3

Mensural characteristics of Laughing Gull eggs, 1975 and 1976, presented as length, width, and weight within one day of laying.

	A egg			B egg			C egg		
	Length mm	Width mm	Weight g	Length mm	Width mm	Weight g	Length mm	Width mm	Weight g
1975 3-egg clutches									
mean	54.2	38.6	43.4	53.9	38.6	43.2	52.1	37.1	39.2
range	48.0–60.6	36.7–40.6	36.1–48.2	49.4–57.6	36.9–40.5	34.6–50.4	47.8–56.7	38.9–44.4	34.2–48.3
SD	2.1	0.9	2.7	1.0	0.9	2.9	2.0	0.9	2.8
n	77	77	60	78	78	59	76	76	60
2-egg clutches									
mean	54.7	38.6	43.3	54.6	38.0	42.9			
range	52.2–57.8	37.4–40.4	38.6–47.0	50.4–57.3	36.1–39.4	35.7–48.7			
SD	1.6	1.0	3.2	2.2	1.2	4.0			
n	12	13	11	13	13	12			
			mean, all eggs	54.3	38.3	42.8			
1976 3-egg clutches									
mean	53.4	38.3	42.5	52.2	38.3	40.9	50.2	36.4	36.3
range	48.3–57.5	36.2–40.6	36.0–47.5	49.4–57.6	35.6–40.5	33.0–48.0	47.8–56.7	34.4–38.9	30.5–41.8
SD	1.9	1.4	2.7	2.0	1.4	2.8	2.4	1.2	3.1
n	78	78	77	78	78	78	78	78	78
2-egg clutches									
mean	53.2	38.0	41.5	51.5	37.2	38.7			
range	47.6–56.8	35.5–40.3	34.5–47.5	40.7–56.3	34.6–45.9	28.5–47.5			
SD	1.9	1.0	2.7	2.7	1.6	3.4			
n	60	60	60	60	60	60			
			mean, all eggs	52.2	37.7	40.0			

Possible Relaying

Of 134 nests in 1976, 11 received a second set of eggs after loss of the first clutch. Since we did not have marked adults, it was impossible to determine if the second set was relaying by the original pair. From observations of behavior we believe that eight of these were relayings; three probably were not.

In four nests second clutches were laid five to 11 days after the first sets disappeared. In three nests second clutches were laid 15 to 30 days after the first set disappeared. In one nest the initial clutch of two disappeared and after five days was replaced by one egg which disappeared after 25 days and was replaced by two more eggs. These last two eggs weighed 32.5 and 31.0 g at laying, exceedingly light for this colony. We do not know if they hatched.

Only one nest received more eggs on the second laying (3) than it received on the first (2). All others received the same number or fewer than the original clutch.

Clutch Size and Egg Size

In 1975, the mean clutch size of 95 nests was 2.84 eggs (Table 2), nearly identical to the 2.83 mean clutch size reported for this colony in 1972 by Dinsmore and Schreiber (1974).

In 1976, we marked nests as soon as we noticed construction beginning. Of 161 marked nests, 138 received eggs and the mean clutch size was 2.52 eggs (Table 2). Mean clutch size was 2.63 in the previously used mid-section of the colony and 2.51 in the newly colonized east section, not a statistically significant difference. Mean clutch size declined insignificantly through the season. Spaans and Spaans (1975) found a decline in clutch size with season in Herring Gulls.

We recorded a mean clutch size of 2.19 for 193 nests on 12 May 1977 (the end of the laying period), the second of only three short visits to the island that year. Clutch size is significantly different (*t*-test, $P < 0.001$) between each of these three years. We cannot explain the higher percentage of 2-egg nests in 1976 (43% vs. 15% in 1975) and even higher in 1977, except that it may be related to the increased nest density, decreased food availability, or use of a poor food source (i.e., garbage dump).

The length, width, and weight of eggs laid in marked nests in 1975 and 1976 are presented in Table 3 and compared statistically in Table 4. In both years, C eggs were significantly smaller than A and B eggs in 3-egg clutches (Table 4). Preston and Preston (1953) had similar results for Laughing Gull egg width. A and B eggs in 1975 and A eggs in 1976 did not vary statistically in size, either within or between 3- and 2-egg clutches. In 1976, B eggs of 2-egg clutches were significantly smaller in width and weight than B eggs of 3-egg clutches. B eggs were also significantly smaller than A eggs in both 2- and 3-egg clutches in 1976. Only in 1976 did a small decrease in egg weight occur through the

TABLE 4

Significance levels (*t*-test) within and between years of mensural characteristics of Laughing Gull eggs.

	Length	Width	Weight
1975			
3-egg clutches	A/B = ns	ns	ns
	B/C = .001	.001	.001
	A/C = .001	.001	.001
2-egg clutches	A/B = ns	ns	ns
3/2-egg clutches	A/A = ns	ns	ns
	B/B = ns	ns	ns
1976			
3-egg clutches	A/B = .001	ns	.001
	B/C = .001	.001	.001
	A/C = .001	.001	.001
2-egg clutches	A/B = .001	.001	.001
3/2-egg clutches	A/A = ns	ns	ns
	B/B = ns	.001	.001
1975/1976			
3-egg clutches	A/A = .02	.07	.07
	B/B = .001	.07	.001
	C/C = .001	.001	.001
2-egg clutches	A/A = .02	.07	.05
	B/B = .01	.05	.01

season and it occurred in A, B, and C eggs equally. Parsons (1972) found a larger average decrease in the size of C eggs compared to A eggs through a single season.

Between-year comparisons are not so straightforward. In 1976, A eggs in 3-egg clutches were significantly shorter but only marginally narrower and lighter than the A egg in 3-egg clutches in 1975. A eggs of 2-egg clutches in 1976 were significantly shorter and lighter but only marginally narrower than A eggs in 2-egg clutches in 1975. In 1976, B and C eggs in 3-egg clutches were significantly smaller than in 1975, as were the B eggs in 2-egg clutches. Additionally, we found a higher percentage decrease in the weight of the B and C eggs between years compared to the decrease in A egg weight (Table 5).

These figures suggest caution when generalizing extensively on egg size as related to other reproductive parameters with only one year's data (Parsons, 1972) and especially when making statements on relative egg sizes of eggs within clutches of Laughing Gulls (Montevecchi, 1976).

Our increased disturbance in 1976, when we checked nests twice a day, probably was not the cause of decreased clutch and egg size that year over 1975 since both continued to decline in 1977 when we made only three brief visits to the island. The data of Kanwisher et al. (1978) on increased heart rates during aggressive activity in Herring Gulls are

TABLE 5

Changes in the proportion of egg weights between years.

	Within year comparisons				
	3-egg clutches		2-egg clutches	A of 2 eggs / A of 3 eggs	B of 2 eggs / B of 3 eggs
	B/A	C/A	B/A		
1975	99%	90%	99%	99%	99%
1976	96%	85%	93%	97%	94%

Between year comparisons					
3-egg clutches			2-egg clutches		All eggs
A eggs 1976 / A eggs 1975	B 1976 / B 1975	C 1976 / C 1975	A 1976 / A 1975	B 1976 / B 1975	1976 / 1975
98%	96%	93%	95%	90%	93%

intriguing. Perhaps the higher density nesting in 1976 and 1977 in this colony caused more disturbance and increased metabolic activity, resulting in less energy in the form of lipid for deposition in the eggs and thus a reduced clutch and egg size.

Studies of other gull species have shown that clutch size tends to be smaller in younger birds (Coulson and White, 1958; Mills, 1973), those with less breeding experience (Coulson and White, 1961), and later nesting birds (Coulson and White, 1961). Mills (1973) and Davis (1975) also suggested that young gulls tend to nest later. Thus, possibly the reduced clutch and egg size we found in 1976 and 1977 was due to more young birds breeding in those years, a facet of the colony for which we have no data. However, since 2-egg clutches were not laid later than 3-egg clutches in any year, nor were they laid on the periphery of the colony, we suggest that age was not a major factor involved here.

Low food availability may well have been the reason for our decrease in egg and clutch size, a cause suggested by Lemmetyinen (1973) and Evans and McNicholl (1972). Possibly also, since the incidence of Laughing Gulls from this colony feeding in local garbage dumps has increased over the past few years, they are not getting the proper nutrition to produce normal clutches. Scott (1973) predicted that when a female bird does not have sufficient protein or essential amino acids in its diet, it will produce smaller and fewer eggs.

The mainland portion of this colony site was developed into a golf course in April and May of 1976. The increased number of 2-egg clutches may have been due to birds displaced from the mainland area laying smaller clutches, but if so, they integrated themselves into the island colony rapidly with no measurable delay.

Incubation Period

We determined the incubation period in 1975 to within 24 hr and in 1976 to within 12 hr (Table 6). Hatching is here defined as the presence

TABLE 6

Incubation periods in Laughing Gulls.

Incubation period (days)	3-egg clutch			2-egg clutch	
	A	B	C	A	B
			1975		
mean	24.0	23.8	23.7	23.9	23.9
SD	0.9	0.7	0.8	0.8	0.8
range	22–26	23–25	23–25	23–25	23–25
n	45	42	36	8	12
			1976[1]		
mean	24.3	24.2	24.0	24.6	24.2
SD	0.7	0.7	0.6	0.4	0.7
range	24–25	23–25.5	23–25	24.5–25	23.5–26
n	12	18	22	7	10

[1] Eggs for which the incubation period is known within 12 hr.

of a wet chick out of its egg. The incubation period for the majority of eggs was 23 to 25 days, with 56% of all eggs incubated over 23.5 days and under 25 days. Parsons (1972, and references therein) found that egg size affected incubation period in Herring Gulls, but in the Laughing Gull we found that heavier eggs were not incubated longer than lighter eggs and no trend in this direction existed.

No seasonal differences existed in incubation period of eggs contrary to the findings of Parsons (1972), MacRoberts and MacRoberts (1972), and Davis (1975). No significant differences existed between the length of incubation for A, B, or C eggs, but more precise determination of the incubation interval and a larger sample size might show statistical differences. Although as the incubation period and size of eggs decrease in smaller gulls, the amount of possible variation decreases; so the variability detectable may be biologically unimportant.

The differences in incubation period between 1975 and 1976 (Table 6) may be due to inconsistencies in checking nests between years. Weather patterns and temperatures were similar in the Tampa Bay region in April–June in the two years (Local Climatological Data, NOAA). Drent (1970) noted that incubation was interrupted by a serious need to preen, such as a beetle crawling over the incubating bird. We noticed an increase in the number of ants in this colony between 1975 and 1976, and possibly the ants interrupt incubation, thus causing an increased incubation period in 1976, especially since their bites kill hatching young and create an infection leaving holes in the toe webs of older birds.

Egg Weight Loss During Incubation

In 1976, the mean weight loss of eggs from the day laid until they were pipped was 14–16% of initial weight (Table 7). This is similar to

TABLE 7

Weight loss in eggs during incubation of Laughing Gulls, 1976.

	A egg			B egg			C egg		
	Weight when laid	Weight when hatched	Grams lost	Weight when laid	Weight when hatched	Grams lost	Weight when laid	Weight when hatched	Grams lost
3-egg clutches									
Mean	42.4	36.6	5.9	40.4	33.9	6.62	36.1	30.3	5.8
SD	2.72	2.88	0.79	2.66	2.93	0.86	2.94	2.92	1.13
Range	37.5–46.0	31.5–40.0	4.5–7.5	36.0–45.0	29.0–39.0	5.0–8.5	31.5–40.5	24.0–36.0	4.0–8.5
n	15			18			21		
% lost			14%			16%			16%
2-egg clutches									
Mean	40.9	34.6	6.3	39.7	33.8	5.9			
SD	2.0	1.72	0.83	2.83	2.48	0.85			
Range	36.0–43.0	31.0–37.5	5.3–7.5	36.5–45.5	30.5–39.0	5.0–7.5			
n	15			13					
% lost			15%			15%			

the findings of Haycock and Threlfall (1975) for Herring Gulls. During the period between development of the first cracks until pipping occurred, a weight loss of 0.4 to 0.8 g (1–2% of the fresh weight) occurred. The mean weight loss was not significantly different for any of the eggs. Fifty percent of the weight loss occurred by the 16th day of incubation, or 66% of the way through incubation. Fifty percent was lost in the last 7–8 days of incubation, including loss after pipping.

Hatching Success

Total hatching success for all nests receiving eggs was similar in both years: 79% in 1975 and 81% in 1976 (Table 8). Hatching success for 3-egg clutches in 1975 was 78% (84% for A eggs, 79% B, and 71% C) and 93% for 2-egg clutches (86% A and 100% B). Hatching success for 3-egg clutches in 1976 was 87% (84% A, 92% B, and 84% C) and 71% for 2-egg clutches (76% A and 66% B). Dinsmore and Schreiber (1974) in this same colony found minimum hatching success in 3-egg clutches to be 74% and 86% in 2-egg clutches, but also listed another 29% as questionable. Thus, actual hatching success in that year was probably higher and similar to our data for 1975 and 1976. We are unaware of other data on hatching success in Laughing Gulls.

Spaans and Spaans (1975) found hatching success in Herring Gulls in 3-, 2-, and 1-egg clutches to be 79%, 70%, and 19%. Brown (1967) reported hatching success for Herring Gulls as 72% in 3-egg clutches and 50% in 2-egg clutches (mean of 66.6%). Haycock and Threlfall (1975) found a mean hatching success in the same species of 73%, with 72%, 78%, and 67% for A, B, and C eggs. Davis (1975) divided hatching success in Herring Gulls into four time intervals throughout the season in each of two years. In 1970, it declined from 79% to 51% and in 1972 from 71% to 63%.

Several studies have reported lower hatching success in smaller clutches (Brown, 1967; Kadlec et al., 1969; Morris et al., 1976) as we found in 1976, but the 93% success in smaller clutches in 1975 was unexpected and may be due to lack of predation that year (see discussion below on failed eggs).

Hatched eggs weighed slightly more initially than those not hatching (A eggs = 1.0 g, B = 0.7 g, C = 0.7 g), and although these differences are not significant, a possible trend exists and the differences could be biologically important (Ricklefs et al., 1978).

In 1976, when we have data for the whole season, hatching success declined during the season in 3-egg clutches (A eggs = 8%, B = 7%, C = 17%) and increased in 2-egg clutches (A = 1%, B = 10%). Spaans and Spaans (1975) and Davis (1975) noted a seasonal decline in hatching success.

No significant difference was found within or between clutches in the length of time eggs took to hatch after the first crack appeared. The mean for all eggs was 2.7 days. Drent (1970) in Herring Gull eggs had a mean first-crack-to-hatching time of 64.1 ± 1.7 hr (3+ days).

TABLE 8

Hatching success in Laughing Gulls in 1975 and 1976.

3-egg nests Eggs hatched	1975 Number hatched	1975 %	1976 Number hatched	1976 %	2-egg nests Eggs hatched	1975 Number hatched	1975 %	1976 Number hatched	1976 %
A, B, & C	45	58	57	75	A & B	12	86	34	59
A & B	13	17	6	8	A	0	—	10	17
B & C	2	3	7	9	B	2	14	4	7
A & C	6	8	0	—	none	0	—	10	17
A	2	3	1	1	Number of nests	14		58	
B	2	3	0	—					
C	3	4	0	—					
none	6	6	5	7					
Number of nests	79		76						

Total of each egg hatching	n	of laid %	n	of laid %	Total of each egg hatching	n	%	n	%
A	66	84	64	84	A	12	86	44	76
B	62	78	70	92	B	14	100	38	66
C	56	71	64	84					
Total laid	237	%	228	%		28	%	116	%
Total Hatching	184	78	198	87		26	93	82	71
Hatch per Nest	2.3		2.6			1.9		1.4	

Cumulative hatching success	1975	1976
Clutch size	2.85	2.57
Total nests	93	134
Total eggs laid	265	344
Total eggs hatched	210	280
Eggs hatched per nest	2.26	2.08
Hatching success	79%	81%

It is difficult to compare figures between species and studies since authors calculate hatching success in different manners and because of investigator bias. Obviously, a need for standardization in data presentation exists. The one comparison it seems safe to make is that hatching success in this colony of Laughing Gulls was high in all years of our study, especially in comparison with other studies of Herring Gulls. We believe this high success is due to the lack of predation in this colony.

Failed Eggs

In our study area 59 eggs (22% of those laid) in 1975 and 68 eggs (20% of those laid) in 1976 did not hatch (Table 9). In 1975, we witnessed no predation but 3% of the total eggs laid disappeared between nest checks. In 1976, we witnessed 16 eggs (5% of those laid) being punctured by other Laughing Gulls in obvious response to our distur-

TABLE 9

Fate of eggs that did not hatch, 1975 and 1976.

		3-egg clutch Number of eggs				2-egg Number of eggs			4-egg Number of eggs	1-egg Number of eggs		Cum. % of eggs laid
		A	B	C	Total	A	B	Total	D	A	Total	
Predated or disappeared	1975	0	1	2	7[1]	1	0	1	0	0	8	3
	1976	8	8	5	21	4	7	11	–	1	33	10
Broken	1975	0	0	2	2	0	0	0	0	0	2	8
	1976	0	0	0	0	1	0	1	–	0	1	.2
Failed-to-hatch	1975	11	15	15	41	1	0	1	0	0	42	16
	1976	11	2	6	19	5	3	8	–	0	27	8
Died pipping	1975	3	1	2	6	0	0	0	1	0	7	3
	1976	0	0	2	2	3	2	5	–	0	7	2
Total	1975	14	17	21	56	2	0	2	1	1	59	22
% of eggs laid (265)		6	7	9	24	.8	0	.8	.4	0		
Total	1976	19	10	13	42	13	12	25	–	1	68	20
% of eggs laid (344)		8	4	6	18	6	5	11	–	.4		

[1] Sequence in clutch was not known for four eggs that disappeared.

TABLE 10

Fledging success in Laughing Gulls in enclosures, 1976.

		Fledglings from each egg	Percent of eggs that fledged young
3-egg nests			
	A	15	60
	B	12	48
	C	6	24
	total	33	
2-egg nests			
	A	9	53
	B	3	18
	total	12	

Summary	Nests with 3 eggs	Nests with 2 eggs	Total
Total nests	25	17	42
Total eggs laid	75	34	109
Number hatched	69	26	95
Percent hatched	92%	75%	87%
Number young fledged	33	12	45
Percent eggs laid that fledged	44%	36%	41%
Percent eggs hatched that fledged	48%	46%	47%
Number of successful nests	22	11	33
Percent of successful nests	88%	65%	78%
Number fledged per successful nest	1.5	1.1	1.36
Number fledged per total nests	1.3	0.7	1.1

bance. The other 5% in this category in 1976 disappeared between nest checks. Apparently no selective predation occurred on A, B, or C eggs or in 2- vs. 3-egg clutches. No differences exist in the mean weight of predated eggs and the mean weight for all eggs laid.

We believe the increased percentage of eggs predated or disappeared in 1976 was due to two causes, increased nesting density and our increased disturbance. We have never seen cats, rats, snakes, dogs, or skeletons thereof in this colony, and during the two years of this study we never saw another human enter the colony. We also never saw any avian predators other than the Laughing Gulls themselves, which we believe were the sole cause of disappearing and predated eggs.

For Herring Gulls, Haycock and Threlfall (1975) had 10% of the total eggs laid lost due to predation, and Drent (1970) had significantly higher predation on 1-, 2-, and 4-egg clutches than on 3-egg clutches. Ryder (1975) noted that nesting immature Ring-billed Gulls lose more eggs to predation than older birds due to less persistent incubation. Fordham (1964) found that high density nesting in southern Great Black-backed Gulls (*L. marinus*) caused extensive egg loss.

The three eggs found broken were thin-shelled. We do not know the cause but it may be related to the decreasing egg and clutch size.

The eggs in the failed-to-hatch category were all incubated full term. In 1975, 42 eggs (16% of those laid) failed to hatch and of these 80% showed no embryonic development. Haycock and Threlfall (1975) had 6% not hatching, and Drent (1970) had 13.7% addled. We do not know why a higher percentage of eggs were in the failed-to-hatch category in 1975 than in 1976. Perhaps a greater percentage of young, inexperienced breeders were able to incubate their eggs, even infertile ones, full term in 1975 since nesting density was lower that year. In 1976, these marginal breeders may have been too disturbed to protect their nests and thus lost more eggs to predation.

Three percent of all eggs laid in 1975 and 2% in 1976 were categorized as died pipping. Drent (1970) had 1.7% die hatching, and Haycock and Threlfall (1975) had 7%. The latter accredited death while pipping to parental behavior. We attributed two to three deaths while pipping each year to ant bites from ants that entered the pip.

We found only one egg in a nest encapsulated by half the shell of a hatched sibling. Few shell pieces were found in the colony, so it appears that shell removal is a strong tendency. Montevecchi (1976) suggested that shell removal by Laughing Gulls could aid in prevention of nestling injuries and encapsulation of other eggs.

Fledging Success

Since we had to release our enclosed chicks in 1975, we have no data on fledging success for that year. In 1976, the number of young fledged per total nests receiving eggs was 1.32 for 3-egg clutches and 0.71 for 2-egg clutches (Table 10). Of the eggs laid in 3-egg nests, 44% fledged a young whereas 36% of those in 2-egg nests did so. Of 3-egg nests 88% were successful at fledging one or more young whereas 65% of 2-egg nests were successful. For details on the success of A, B, and C eggs refer to Table 10.

Several studies of Herring Gulls (Davis, 1975; Parsons, 1975) and one of Laughing Gulls (Spaans and Spaans, 1975) have shown higher survival for young from A and B eggs than from C eggs, as we found (Table 10).

In 3-egg clutches the mean weight of C eggs that fledged a young tended to be higher than the mean weight of all C eggs (38.0 g, $n = 6$, vs. 36.3 g, $n = 77$). There was no difference in A and B eggs.

In 2-egg clutches B eggs from which a young fledged were significantly heavier than the mean for all B eggs (40.8 g, $n = 3$, vs. 38.7 g, $n = 50$, t-test, $P < 0.01$), but this is a small sample size. There was no difference in A eggs.

We found no difference in the mean hatching weights of chicks that fledged and those that did not. Some of the newly hatched chicks may have been fed before we weighed them for the first time. However, we would not expect a feeding difference in one group compared with the other. Davis (1975) found that survivorship of Herring Gull chicks increased with hatching weight and that young from A and B eggs tended to survive better than those from C eggs. Parsons (1975) found that hatching weight declined with order of laying and C young had lower survivorship than chicks from A or B eggs.

CONCLUSIONS

An interesting phenomenon is occurring in this Laughing Gull colony, manifested in increasing nest density, decreasing egg size, and decreasing clutch size. Incubation period apparently was not affected but accurate determination of this time span is difficult. No other study has reported decreasing egg and clutch size, even in Herring and Ring-billed gull colonies that have increased in size so dramatically in the last few years. This may indicate that increased nest density is not a factor causing our decreasing egg and clutch size.

A change in food and feeding habits might be a causal factor in the decreasing egg and clutch size but without nutritional studies this is impossible to determine. Increased feeding in garbage dumps has occurred in other gull populations as well as this one. If this feeding habit change could cause decreased egg and clutch size, we would expect these phenomena to have been noted in other gull colonies as well.

In Part II, egg parameters will be discussed in relationship to growth and development and survivorship of young.

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