J. Field Ornithol., 51(4):340–355

BREEDING BIOLOGY OF LAUGHING GULLS IN FLORIDA. PART II: NESTLING PARAMETERS

By Elizabeth Anne Schreiber and Ralph W. Schreiber

This paper presents data on nestling Laughing Gulls (*Larus atricilla*) and continues the presentation of Schreiber et al. (1979). We analyze growth and fledging success by sequence in clutch, brood size, time of nesting, and hatching weight. Growth of juvenal plumage is described and related to growth rate. The causes of mortality in nestlings are described.

STUDY AREA AND METHODS

Our study area and methodology were described in Schreiber et al. (1979). As noted there, nestlings had to be released in 1975 and thus growth and fledging data were lost for that year. Here we discuss growth of 1976 nestlings.

Growth rates were determined by comparison to the weight growth curve for the colony (Fig. 1) and divided into three categories for analysis: fast, mean, and slow. Fast-growing chicks had a growth curve between the upper range and the upper standard deviation of the curve in Fig. 1. Mean growth was between the two standard deviations from the mean, and slow growth was below the lower standard deviation.

For analysis of fledging success by seasonal timing, the season was divided into three periods according to when eggs were laid. Early clutches were begun before the peak of laying, middle clutches were begun during the 10-day peak of laying (Schreiber et al. 1979), and late clutches were begun after the peak of laying.

We use c/1, c/2, and c/3 to indicate clutch size, and b/1, b/2, and b/3 to indicate brood size. A b/1 could consist of the surviving chick of a c/3, and is not necessarily from a c/1. These notations do not indicate sequence in clutch or brood.

RESULTS AND DISCUSSION

Growth of chicks.—Figures 1, 2, and 3 show mean, standard deviation, and range of weight, culmen, wing (unflattened chord), tarsus (external, Schreiber 1970), and tail for Laughing Gull chicks in 1976. These data are from known-age chicks in our study areas. Measurements for adults are from 50 birds captured alive in the colony or found freshly dead in Pinellas County. Further data on Laughing Gull meristics are in Schreiber and Schreiber (1979).

Chicks weighed 25 to 35 g at hatching (Fig. 1), approximately 10% of adult weight (Fig. 4). Weight increased rapidly until about day 30 when asymptotic weight was reached. Fledging occurred between 38 and 50 days, and in general, the chicks which increased in weight fastest fledged earliest. Most weighed more than the adult mean at fledging.

Culmen length (Fig. 2) ranged from 13 to 16 mm at hatching, 35%

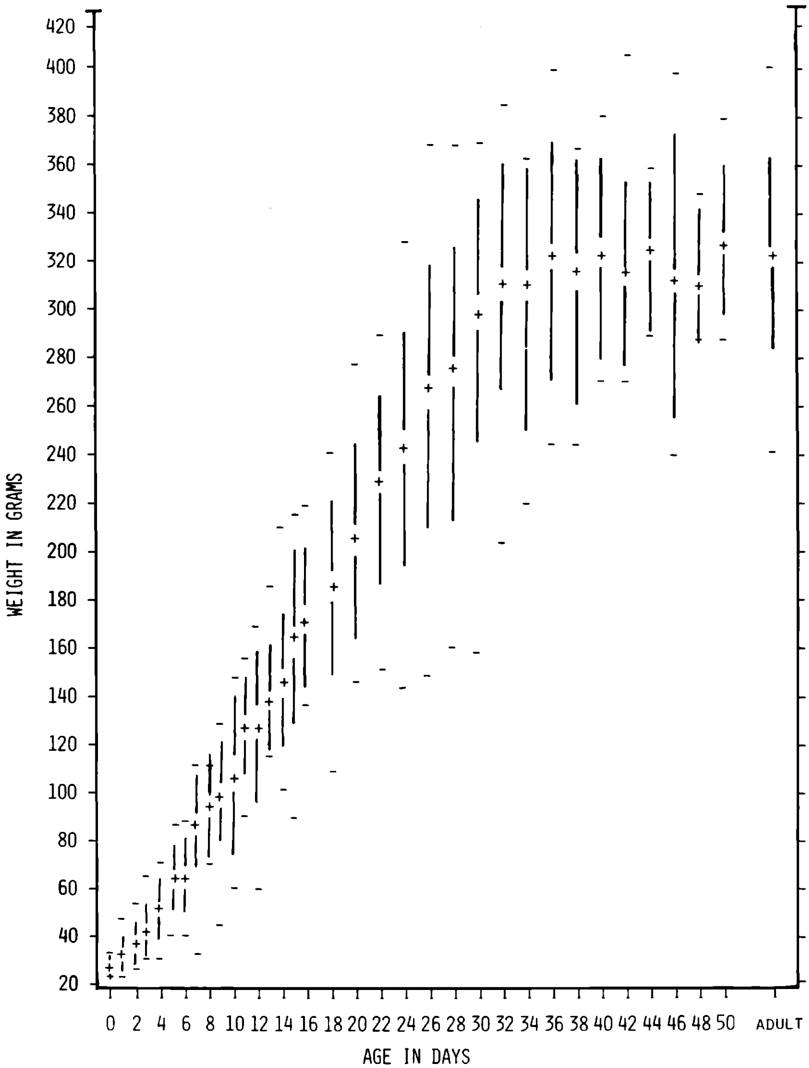

FIGURE 1. Changes in weight with age in chicks. Vertical lines indicate one standard deviation above and below the mean. Horizontal dashes indicate the range. Day 0 to 36 (1st fledging), n = 65 to 21. Day 37 to 50, n = 16 to 6.

of adult length, and increased in a straight line until about day 12, when growth slowed. The culmen appears to have the most steady, constant growth rate and was 88% of adult size at fledging (Fig. 4).

The tarsus (Fig. 2) ranged from 23 to 28 mm at hatching, 45% of adult size (Fig. 4). Growth was rapid for two weeks, slowed, reached asymptote at day 36 and the tarsus was adult size at fledging.

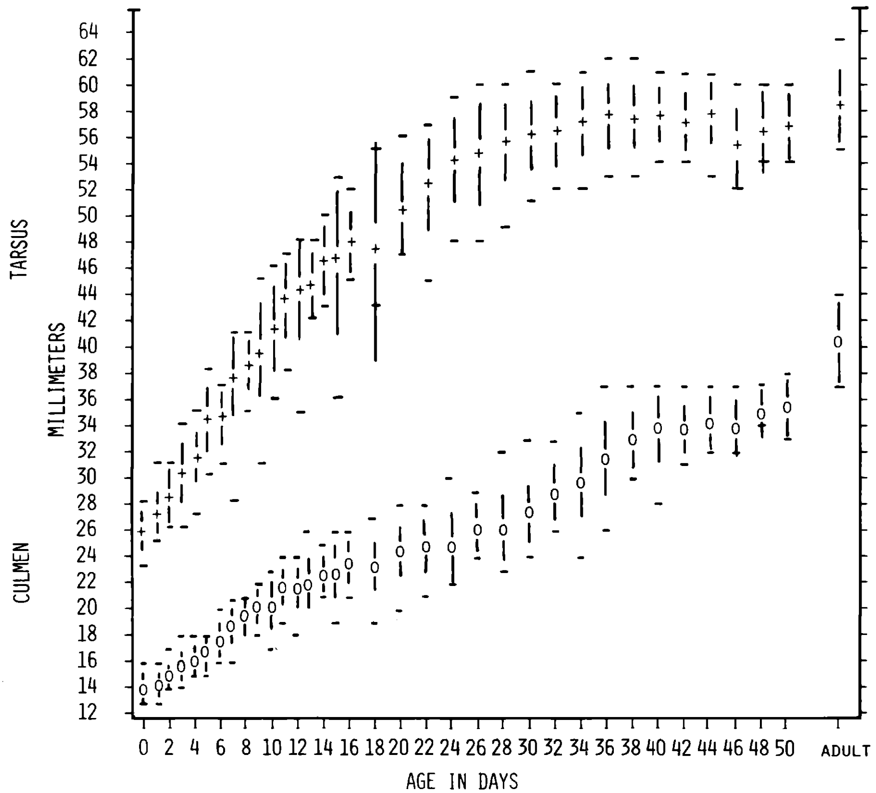

FIGURE 2. Changes in culmen and tarsus length with age in chicks. Horizontal lines indicate one standard deviation above and below the mean. Vertical dashes indicate the range. Day 0 to 36 (1st fledging), n = 65 to 21. Day 37 to 50, n = 16 to 6.

Wing length (Fig. 3) increased relatively slowly from hatching ($\bar{x}$ = 19.3) until day 14 when growth rate increased greatly. This occurred when culmen and tarsus growth were slowing. Wing length was 81% of adult size at fledging and reached adult size by 55 to 60 days.

Rectrices (Fig. 3) first appeared at day 13 and after slow growth for one week, grew rapidly to day 42. The tail was 88% of adult length at fledging.

These growth parameters are essentially those found by Dinsmore and Schreiber (1974) for captive raised chicks except that captives reached asymptotic weight and tarsus length several days earlier than wild chicks. While these differences were slight and based on four captive chicks, they perhaps do indicate that readily abundant food (as was available to the captives) allows faster growth and that tarsus length is more tied to weight than are culmen and wing lengths.

No difference existed in the mean asymptotic weight reached by our

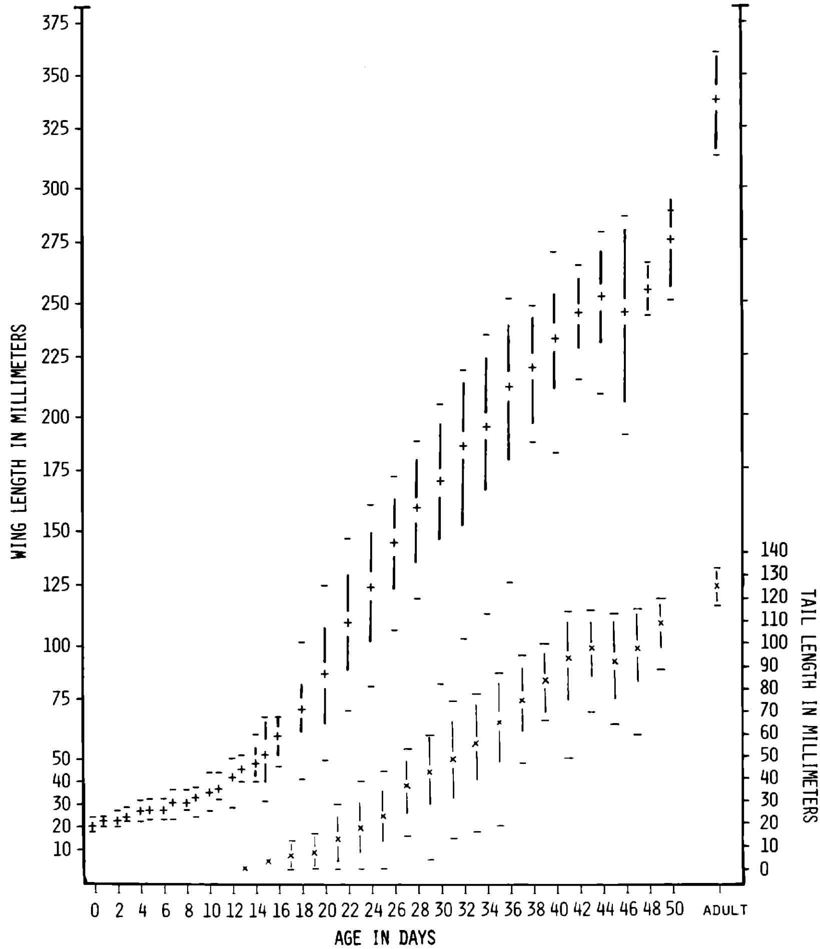

FIGURE 3. Changes in wing and tail length with age in chicks. Vertical lines indicate one standard deviation above and below the mean. Horizontal dashes indicate the range. Day 0 to 36 (1st fledging), n = 65 to 21. Day 37 to 50, n = 16 to 6.

chicks in b/1 and b/2 (340 g); however, chicks in b/2 averaged two days longer to reach this weight (36 vs. 34 days). In our two b/3, the chicks were still gaining weight when last measured; their mean weight was 309 g at a mean age of 36 days.

Ricklefs (1968) suggested that poor nutrition may reduce asymptotic weight but had no evidence that the growth rate was affected except when young starved. Our data suggest that growth rate is affected by nutrition, but that asymptote for all growth parameters is not. Haycock and Threlfall (1975) suggested that the sexes in the Herring Gull (*Larus*

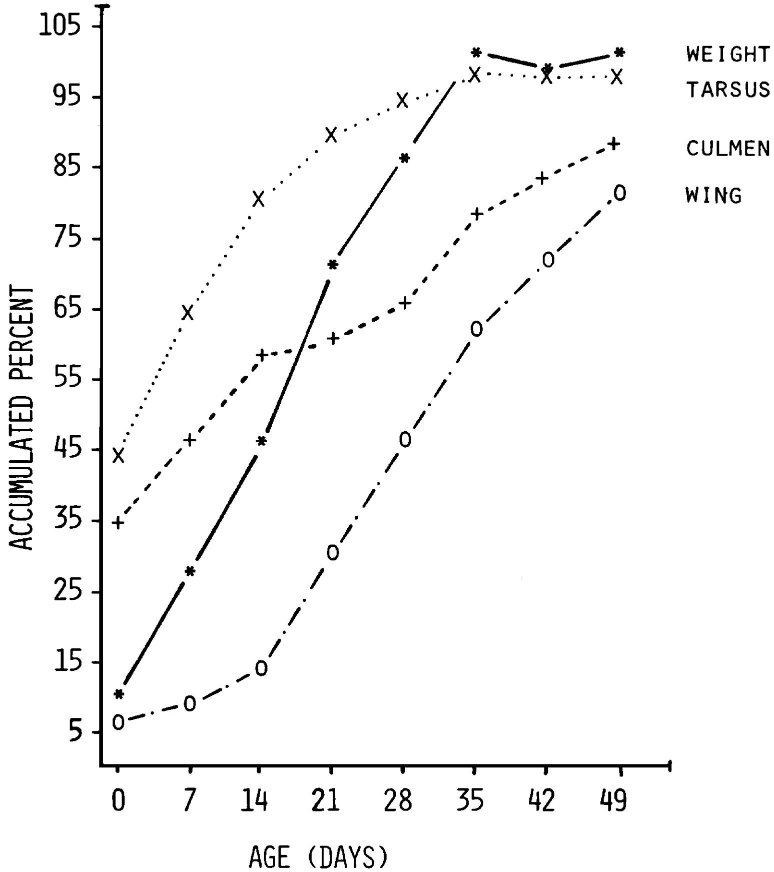

FIGURE 4. Accumulated increase in weight and linear measurements of chicks, represented as a percentage of adult measurements. Day 0 to 36, n = 65 to 21. Day 37 to 50, n = 16 to 6.

argentatus) may fledge at different weights, since they show distinct sexual dimorphism. The Laughing Gull is a much smaller bird with a high degree of size overlap between sexes (Schreiber and Schreiber 1979), and the variability in weight would not be expected to reflect sexual differences.

We found no relationship between hatching weight and chick growth rates. Growth curves for chicks that fledged showed no periods of erratic growth. Most chicks that died did so by day 7, and chicks dying after that usually had slow growth or erratic growth rates. We could not determine the reasons for slow or erratic growth, but assume it was due to parental inability to provide food, the death of one parent, or inexperienced parents. We lost only five chicks with mean growth rates after day 10: one from pecking, one from a broken wing, and three of unknown causes.

In 13 nests (9 c/3 and 4 c/2) one egg remained in the nest after the other(s) hatched. The presence of this egg did not affect sibling survival, and growth rates for chicks in these nests were comparable to mean growth for the colony.

Feather growth.—The scapular feathers were the first of the juvenal plumage to appear. Sheaths emerged at day 5–8; unfurled feathers were 6–20 mm long at day 10, up to 50 mm by day 20, and 90 mm (full length) at day 30. Maximum feather sheath length of 13 mm was reached at day 14–15, and the sheaths were gone by day 22–25.

We measured primary feather number 10 up to day 12–14 while it was the longest primary, but after that we used number 8, which became longer. Primary growth (Table 1) closely paralleled that of the wing shown in Figure 3, with feather sheaths first appearing at day 8–11. Primaries ranged from 140 to 205 mm at fledging; adult primary length is 230 mm ±5%. Maximum sheath length of 45–47 mm was reached at day 26–43, and sheaths were gone by day 42–48.

No rectrices appeared before day 13 (Table 1) and some not until day 23. Rectrices were still growing at fledging, and ranged from 70–120 mm; adult length is 125 mm ±5%. Maximum sheath length of 28–30 mm was reached between day 28–44, and sheaths were gone at fledging.

Covert feathers first appeared in chicks at day 8–11 and secondaries at day 9–11. We have no further data on growth of these feathers. Scapulars appeared more consistent in timing of appearance and growth than did flight feathers. This may be related to a possible thermoregulatory function of scapulars in chicks.

Down remained on the primary, secondary, and rectrix feather tips until about day 20. The body obviously was losing down at day 20–25 while all chicks were fully downy prior to then. By day 30, down remained only on the belly, rump, inner legs, neck, and head. By day 40, down remained only on the flanks of some birds. At fledging, all down was gone.

Primary, secondary, and rectrix growth was highly variable and was related to food/energy availability. Laughing Gull chicks which consistently weighed less than the mean for their age showed slow feather growth, as Parsons (1971) also found in the Herring Gull. Chicks which weighed more than the mean for their age had more well-developed feathers.

Estimating the age of chicks from growth curves.—From our growth curves we can predict the age of chicks up to a week old to within 2 days, within 3 days for chicks 1 to 3 weeks old, within 4 days for chicks between 3 and 4 weeks of age, and within 5 days for chicks older than 4 weeks. This estimation is done using culmen, tarsus, wing, tail, and weight measurements together. Much less accuracy is obtained when any one of these measurements is eliminated. Knowing feather length also improved age estimates. As LeCroy and LeCroy (1974) demonstrated in

TABLE 1.
Growth of Laughing Gull feathers.

Day	Primaries* Mean	Range	SD	N	Rectrices** Mean	Range	SD	N
8–9	2.1	0–5	2.9	9	0	0		
10–11	3.5	0–5	2.6	14	0	0		
12–13	8.6	6–11	2.8	22	2.2	5	2.0	6
14–15	13.4	0–23	7.9	39	7.0	20	6.3	7
16–17	21.3	8–38	8.9	25	7.5	17	5.2	12
18–19	28.9	8–47	11.4	27	5.5	—	5.1	10
20–21	42.4	17–64	11.7	27	15.6	0–30	8.8	9
22–23	57.1	34–80	16.9	14	19.1	0–40	11.8	8
24–25	66.3	37–90	15.5	27	24.2	0–44	10.6	16
26–27	84.4	55–105	16.4	25	37.1	16–54	10.9	16
28–29	92.4	26–115	20.3	21	43.8	5–60	16.5	17
30–31	103.9	40–135	21.4	28	49.7	15–75	16.2	25
32–33	115.3	40–155	19.8	23	57.5	17–77	15.9	25
34–35	131.5	65–152	19.8	23	66.5	20–88	17.3	22
36–37	142.6	113–160	14.6	23	76.1	47–95	14.3	22
38–39	148.6	130–165	13.8	18	83.7	67–100	10.9	18
40–41	162.8	113–183	18.1	14	93.4	50–115	16.6	14
42–43	167.0	140–195	13.5	16	97.6	70–115	13.3	15
44–45	175.0	160–185	12.2	4	92.5	65–105	18.5	4
46–47	165.7	135–190	18.6	7	96.9	60–115	18.2	7
48–49	186.7	170–205	14.0	6	109.2	88–120	13.9	6
adult	227.2		7.0	9	124.7		3.9	6

* Longest primary was measured: number 10 through day 12–14, number 8 thereafter.
** Longest central rectrix was measured.

terns, weight and wing length alone are not reliable for estimating chick age, and they also found growth rates to be inconsistent between years. We urge use of all available chick growth measures to estimate age of chicks.

Chick mortality.—In Table 2 we present data from our enclosures on chick mortality by sequence in clutch, clutch size, and reason for death. We believe these data for 25 c/3 and 17 c/2 are representative of events in the whole colony. They paralleled our mortality results in open marked areas where many data were lost without captive chicks.

Fifty-two chicks (54% of those hatched) died; 77% of these did so during the first 7 days. B and C chicks showed higher mortality than A chicks. Other studies of Larids indicate, as we found, that highest mortality is in the first week of life (e.g., Kadlec and Drury 1968, Haycock and Threlfall 1975, Morris et al. 1976).

We categorized cause of death when we found dead chicks, or recorded them as "disappeared" if we could not find them prior to an age at which they could have fledged. Determining the cause of death was

TABLE 2.

Causes of death of chicks in enclosed nests, 1976.

Reason for death	Sequence in clutch													
	3-egg clutches						2-egg clutches							
	A		B		C		A		B		Total			
	#	%[1]	#	%[1]	#	%[1]	#	%[1]	#	%[1]	#	%[1]	%[2]
Died pipping	0	—	0	—	1	4	1	7	1	8	3	3	6
Died on day 0	1	5	1	4	3	8	0	—	1	8	6	6	12
Presumed starved, day 1–7	2	10	1	4	2	8	2	13	1	8	8	8	15
Presumed starved, day 8+	0	—	1	4	1	4	0	—	1	8	3	3	6
Pecked, day 1–7	0	—	1	4	2	8	0	—	1	8	4	4	8
Pecked, day 8+	1	5	0	—	0	—	1	7	0	—	2	2	4
Unknown, day 1–7[4]	1	5	6	25	6	25	2	13	2	15	17	18	33
Unknown, day 8+	0	—	1	4	2	8	0	—	2	15	5	5	10
Disappeared, day 1–7[3]	0	—	0	—	1	4	0	—	1	8	2	2	4
Disappeared, day 8+	0	—	1	4	0	—	0	—	0	—	1	1	2
Broken wing, day 16–20	1	5	0	—	0	—	0	—	0	—	1	1	2
Total dead, day 0–7	4	20	9	38	15	63	5	33	7	54	40	41	77
Total dead, day 8+	2	10	3	13	3	13	1	7	3	23	12	12	23
Total dead	6	29	12	50	18	75	6	40	10	77	52	54	100
Total chicks hatched	21		24		24		15		13		97	100	
Total eggs laid	25		25		25		17		17				

[1] Percentage based on total number of chicks that hatched.
[2] Percentage based on total number of chicks that died.
[3] Disappeared = out of enclosure and too young to have fledged.
[4] Unknown = not underweight or pecked.

difficult, since it was impossible in many cases to differentiate between starvation, being pecked, disease, or genetic factors. We give our best estimate.

Three chicks died pipping (one A, B, and C), and six died of unknown causes on the day they hatched (3 were C chicks). We categorized 21% of the dead chicks as dying of starvation; of those, 73% died during the first 7 days. Harris (1964) found no chicks to die of starvation and attributed this to the fact that in his study area the Herring, Lesser

TABLE 3.

Fledging success in Laughing Gulls in enclosures, 1976.

3 egg nests			2 egg nests		
Nests producing fledglings	Number of nests	%	Nests producing fledglings	Number of nests	%
A, B, & C	2	8	A & B	1	6
A & B	4	16	A	8	47
B & C	2	8	B	2	12
A & C	1	4	None fledged	4	24
A	8	32	None hatched	2	12
B	4	16	Number of nests	17	
C	1	4			
None fledged	3	12			
Number of nests	25				
Fledglings from each egg	#	%[1]		#	%[1]
A	15	60	A	9	53
B	12	48	B	3	18
C	6	24			
Total fledged	33			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%	76%	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	1.09	1.36
Number fledged per total nests	1.32	0.71	1.07

[1] Percentage of eggs laid in that clutch sequence that fledged a chick.

Black-backed (*Larus marinus*), and Great Black-backed (*Larus fuscus*) gulls live off man's waste. Our Laughing Gulls feed in the local dumps (Schreiber et al. 1979), but this apparently unlimited food supply did not prevent chick starvation. Starvation could be due to inexperienced adults unable to catch enough food to feed their young, too many young to adequately feed, inappropriate change of behavior from incubating to brooding and feeding, or feeding chicks non-nutritional food such as is obtained in garbage dumps (cf. Schreiber et al. 1979).

TABLE 4.
Fledging success by growth rate of chicks and brood size.

	Brood size						
	3 chicks		2 chicks		1 chick		Total
Growth rate	#	%[1]	#	%[1]	#	%[1]	#
Fast	1	11	7	20	7	25	15
Mean	7	78	25	74	19	68	51
Slow	1	11	2	6	2	7	5
Total chicks	9	13[2]	34	48[2]	28	39[2]	71
Number of nests	3	9[3]	17	34[3]	28	58[3]	48

[1] Percentage of number of chicks in that brood size.
[2] Percentage of total number of chicks (71).
[3] Percentage of total number of nests (48).

Heavy rain on 20–22 May caused the death in the whole study area of at least 8 chicks up to 4 days old. More storm-caused mortality is possible but was difficult to confirm. During this storm, few adults were seen feeding chicks and few chicks regurgitated when handled. We did not check nests while it was raining to prevent wetting the chicks. Chilling probably contributed to chick mortality, however, as was found by Haycock and Threlfall (1975). White et al. (1976) noted that exposure to cold and wet along with a lack of food during storms caused increased mortality in Sooty Tern (*Sterna fuscata*) chicks, especially in younger ones.

Of chicks found dead, 12% had bloody heads from pecks by adults or other pulli, and 67% of these were under 8 days old. None was underweight or starving. The pecking may be due to poor nest locality, chance, or wandering by chicks. Our data indicate less pecking of chicks, and thus lower mortality, in our enclosures than in the open study areas, probably because chicks in the enclosures could not wander as far from their nests when disturbed by us. Adults also tended to not return to the enclosures until after we left and chicks had started to return to their nest sites. Thus, the chicks' chances of encountering territorial adults were decreased. Gillett et al. (1975) found increased egg and chick mortality in a Glaucous-winged Gull colony (*Larus glaucescens*) in more disturbed areas. Hunt and McLoon (1975) hypothesized that chicks, but especially C chicks, wandered because of starvation and thus were more susceptible to attack by neighboring birds. We did not find that C chicks were significantly more affected by pecking than others.

Forty-three percent of dead chicks died from undetermined causes which could be due to genetic defects, disease, or internal parasites. One chick disappeared from our enclosures before it was 20 days old and was presumed dead. One was found with a broken wing at 16–20 days and died.

TABLE 5.

Fledging success related to growth rate of chicks and timing of the nesting season.

	Period of the nesting season							
	Early		Middle		Late		Total	
	#	%[1]	#	%[1]	#	%[1]	#	%[1]
Growth rate								
Fast	4	27	7	16	4	31	15	21
Mean	11	73	32	74	8	62	51	72
Slow	0	—	4	9	1	8	5	7
Total	15	21[2]	43	61[2]	13	18[2]	71	

[1] Percent of total in that category.
[2] Percent of 71, the total fledged.

No evidence of predation existed in this colony (see Schreiber et al. 1979), probably because humans rarely visited it during a breeding season and no mammals were present on the island.

Since methodologies vary so greatly, it is difficult to compare data between Larid studies in a meaningful way. Gillett et al. (1975) figured mortality by checking their Glaucous-winged Gull colony study area for dead chicks once per week and found 26.5% of hatching chicks dead. In a control area, checked only twice in the season, they found 11.2% mortality. This method probably gives a low estimate, especially in areas visited less frequently, since chick carcasses in our experience disappear within 2 to 5 days.

Kadlec et al. (1969) felt that chick mortality from all causes until young are partially independent is fundamentally a result of an incomplete

TABLE 6.

Fledging success related to growth rate of chicks and sequence in the clutch.

	Clutch size								
	3 eggs				2 eggs				
	A	B	C	%	A	B	%	Total	Percent of total
Growth rate									
Fast	9	3	0	80	3	0	20	15	21
Mean	16	13	5	67	10	7	33	51	72
Slow	0	2	1	60	0	2	40	5	7
Percent of total	35	25	8	69	18	13	31		100
Total	25	18	6	49	13	9	22	71	

behavior transition of the adults from incubation to brooding and feeding. However, if this were true, we would expect the first chick to hatch to suffer the most, since that time would be the most difficult if the adults were making a behavior transition. By the time the 2nd and 3rd chicks hatch, adults should be able to more effectively feed these later young.

Fledging success.—In our enclosures, 21% (9 of 42) of the nests were unsuccessful (Table 3), with 88% of c/3 and 65% of c/2 being successful. Young fledged per successful nest was 1.4 and 1.1 per total nests. Hatching success for the whole colony was 81% and for enclosed nests 87%. Fledging success in the enclosures was probably higher than outside, but we could not determine fledging success per egg laid or hatched outside the enclosures.

Hunt and Hunt (1976) estimated fledging success in Glaucous-winged Gulls by the number of chicks that reached 500 g in weight: 74% in 1973 and 52% in 1971. Kadlec and Drury (1968) had 0.8 to 1.4 Herring Gulls fledge per nest in different years; Harris (1964) had 0.6 per nest; Parsons (1971) had 0.7 to 0.9 per nest; Davis (1975) had 0.6 to 0.7 per nest; Haycock and Threlfall (1975) had 0.95 per nest. Our fledging success of 1.1 per nest appears high compared to most of these. It may be that our enclosed nests were more successful or that the lack of predation in this colony accounts for the high success. Haycock and Threlfall (1975) found no differences in success between free and penned chicks.

Three egg clutches had higher hatching success, but c/3 and c/2 were essentially equally successful in raising chicks once they hatched. Kadlec et al. (1969) found that c/2 sometimes had as high or higher success than c/3 in Herring Gulls. This is interesting in light of the fact that several studies have found that younger, less experienced birds tend to have smaller clutch sizes (Drost et al. 1961, and others). It may be that in our colony and that of Kadlec et al. (1969) the smaller clutches are not laid by younger birds or that younger birds are not less successful in these colonies.

Age at fledging was set as the last day a chick was found in the enclosure after it reached at least 32 days of age (before which no chick could fly). Since we checked nests only every 3 to 4 days, the exact fledging age could vary by 1–3 days. Mean age of fledging was 42.5 days; range 35 to 50 days. A, B, and C chicks were not significantly different in fledging age in our sample. Age at fledging seemed to be determined by growth rate; slow-growers take longer. Nisbet (1976) had Laughing Gulls fledging at 34 days. None of our chicks was capable of strong flight at that age.

Chicks that fledged tended to have higher hatching weights, although differences were not consistent nor significant where they did occur. Undoubtedly much variation in growth rates occurs from year to year due to variation in environmental factors, food abundance, and colony density.

As with hatching success (Schreiber et al. 1979), we could not determine any seasonal variation in fledging success. A eggs in c/3 were the most successful with 60% of the eggs laid fledging a young. Only 24% of C eggs laid did so (Table 3). This may be due to the smaller size of C eggs and the hatching interval between A–B and C eggs. Producing a small chick that is not likely to survive may be an adaptation to a fluctuating food source and act as an "insurance policy" (Lack 1954, 1968; Ricklefs et al. 1978), but this does not explain why B eggs, c/2, were the least successful eggs in our study, with only 18% of those laid producing a fledgling.

Egg size declined between 1975 and 1976 (Schreiber et al. 1979) resulting in B eggs, c/2, being significantly smaller ($P < 0.001$) than B eggs, c/3. However, B eggs, c/2, were still significantly larger than C eggs ($P < 0.001$) as was the case in 1975, so that we would not have expected them to be less successful than C eggs.

Without known-aged, banded adults and data on food availability, we cannot explain the increase in proportion of c/2 between 1975 (15%) and 1976 (42%), and the poor success of these smaller clutches (see Schreiber et al. 1979, for discussion). LeCroy and LeCroy (1974) reported a decrease in egg and clutch size in a Common Tern colony in 1970, accompanied by reduced chick growth, especially in C chicks. They attributed this to a reduced food supply that year.

Fledging success of chicks as related to growth rate and brood size.—We found a trend for b/1 and b/2 to have a higher percentage of fast-growing chicks than b/3, but the brood size did not significantly affect growth rates (Table 4). Hunt and Hunt (1976) found in one year of a two year study in Glaucous-winged Gulls, that chicks from small broods grew no faster than chicks in large broods.

Fledging success related to growth rate and timing of the nesting season.—We compared growth rates of chicks that fledged with seasonal timing of nests and found very little evidence of seasonal changes in growth rate (Table 5). There were no slow-growing chicks early in the season, and a higher percentage of fast-growing chicks early and late in the season than during the middle but these were not significant differences. All early and late fast-growing chicks were A chicks.

Hunt and Hunt (1976) found growth rate to be the best predictor of survival, followed by timing of hatching, in the Glaucous-winged Gull. Our findings agree with this: higher success in early and middle season nests, and in chicks with fast and mean growth rates.

Fledging success related to growth rate and sequence in clutch.—More A chicks from c/3 fledged than any other category and no A chicks grew at a slow rate. C chicks were the least successful and none grew at a fast rate. Of the fast-growing chicks a higher proportion came from c/3 (80%) and there was a trend for more slow-growing chicks in c/2. This again reflects the lowered success we found in c/2 in this colony in 1976 (Table 6).

Fledging success related to difference in weights of siblings at hatching.—We attempted to correlate chick within-nest survival with weight differences among siblings at the time the 2nd or 3rd hatched but so much variation existed in the weight differences that we found it impossible to predict chick survival by this method. Spellerberg (1971) found that second chick survival was correlated with the weight differences between the chicks at the time the second chick hatched in the McCormick Skua (*Catharacta maccormicki*). It may be that in a bird as large as a skua a large difference in sibling weights is important.

SUMMARY AND CONCLUSIONS

Our findings for Laughing Gulls show that c/3 are generally more successful than c/2 with A eggs—c/3 being most successful; early and mid-season nests are more successful than late; chicks with fast and mean growth rates have higher survivorship; and brood size did not affect growth rates significantly. Fledging success in c/3 was 1.3 and in c/2 was 0.7, with a combined success of 1.1 chicks per nest.

Even without predation in this colony we had a difficult time determining causes of chick death, with 43% dying from unknown causes, 21% presumed starved, 18% dying at hatching, 12% pecked to death, and 8% other.

We found great natural variability in our gull growth patterns, rates, and behavior, and attempting to categorize types was difficult or impossible. Larger sample sizes are needed over probably at least 5 years, especially since any one year is as likely to be the exception as the rule. Any conclusions about chick growth have to take into consideration experience and age of parents, colony location and age, nest site location, and perhaps most importantly, food supply.

Morris et al. (1976) urged caution when considering reproductive success and factors influencing it, saying that no single factor alone can account for observed differences. Robert and Ralph (1975) found that for every trend observed in some plots others contradicted it, so that it was impossible to determine what characteristics made some plots more or less successful.

The question of why so much variation exists in growth is an interesting one. It could be an indication of parental quality, age or experience, nest site quality, or genotypic differences in young. In order to determine the causes of variation, the next step in Larid breeding biology studies would appear to be experimentation: switching eggs and neonates among nests, altering hatching intervals within nests, and reducing and increasing brood size.

Great variation also exists in techniques of ornithologists carrying out field studies. In reviewing the Larid literature we found it difficult, and often impossible, to compare results in a broad manner. Additionally, investigator bias and the need for a large sample size have been ignored by most researchers. An effort needs to be made to standardize field techniques and data presentation methods in future studies. Two other aspects that would lead to a greater understanding of breeding biology in gulls (and other birds) are physiological studies and determination of true food availability.

ACKNOWLEDGMENTS

For financial assistance we are indebted to: the Joint Scientific Staffs of the National Audubon Society and the Massachusetts Audubon Society, Ian Nisbet, Sandy Sprunt, the Research Department of the National Audubon Society, Seabird Research, Inc. and its supporters, and especially to J.C. and M.L.C., whose generosity allowed us to live next to the gull colony in 1976. We are indebted to Anne Ferguson, A. Kahana, S. Wolf, and especially Mary Jane and Peggy Ferguson for invaluable field assistance. Glen Woolfenden provided much stimulation and proved patient while we occupied his space at the University of South Florida. Jerry Jackson improved an earlier draft of the ms. Pat Reynolds and Terri Togiai provided typing assistance.

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Ornithology Section, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007. Received 24 Dec. 1979; accepted 20 Sept. 1980.