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REPRODUCTIVE PERFORMANCE AND BODY CONDITION OF EARLIER AND LATER NESTING RING-BILLED GULLS

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In many species of colonial nesting seabirds, pairs that nest later in the season generally produce fewer eggs and young than do pairs which nest earlier (Parsons 1975, McCrimmon 1980). Although the proximate factors that contribute to the above phenomena are likely multiple and interdependent (Burger 1982), the physical condition of individuals appears to be important as a proximate factor governing the timing of nesting (Ashmole 1963, Perrins 1970) and reproductive success (Coulson 1968, King 1972).

In a study of Ring-billed Gulls (*Larus delawarensis*) Ryder and Ryder (1981) showed that reproductive performance decreased in relation to the timing of nesting. In this study, we were interested in determining whether or not the reported lower reproductive success of later nesting Ring-billed Gulls might be related to their relative physical condition, using egg quality (egg size and amount of dry yolk, lipids, and proteins), body weight, and a condition index as criteria.

METHODS

We conducted the study during the 1979 nesting season (May–July) on Granite Island (48°43′N, 88°29′W), Black Bay, northern Lake Superior. The island and colony were described by Ryder (1976). The colony consisted of 2400 pairs of Ring-billed Gulls in 1979. The summit of the island was chosen as the study area for earlier nests because it became free of snow before lower areas on the island. The entire colony became the second study area because we found later nesting birds were distributed throughout the colony.

Each day, beginning on 20 May, we marked each new one-egg clutch on the summit area with a numbered wooden block. Nests were visited only every second or third day, after clutch completion in an effort to reduce any potential deleterious effects on the eggs and birds by our presence. After the peak of clutch initiation between 20–22 May, which we subjectively gauged by the sharp reduction in the number of clutches started, we searched the colony for later started one-egg clutches. These we marked and monitored in the same way as the earlier nests. From these we selected the last 10% to insure that there was a sufficient difference in initiation dates of the earlier and later nests. The later nests used in our analyses were started between 4 June and 9 July.

We marked eggs in sequence laid whenever possible. Maximum length and breadth were measured to the nearest .1 mm with Vernier calipers. Shell thickness was determined to .1 mm with a Starret 1010 dial indicator pocket gauge. The thickness was measured on both ends and the middle of the shell, then averaged. Egg volume was calculated using the formula .489 × max. breadth^2 × length (Ryder 1975). We assessed the amounts of protein and lipid of freshly laid eggs without necessarily being concerned with laying sequence (see Table 2 for sample sizes). Schreiber and Lawrence (1976) found no correlation between the laying sequence of Laughing Gull (*L. atricilla*) eggs in the clutch and the proportion of lipids and protein. Methodology for the analyses follows that outlined in Freeman et al. (1957), Lawrence and Schreiber (1974), and Thomas and Popko (1981).

Body weight and measurements were obtained by live-trapping attending birds in their first week of incubation, using the trap described in Mills and Ryder (1979). The sex of individuals was determined from external measurements (Ryder 1978). Body weight was taken to the nearest .5 g with a 1000 g Pesola hand-held scale. Bill length (Baldwin et al. 1931) and keel length (Harris 1970) of 20 birds were measured .1 mm with Vernier calipers. These morphometric measurements were used to compute the Condition Index (body weight (g)/(bill length (cm) + keel length (cm))) devised for gulls by G. Fox (pers. comm.). The index is useful because it considers structural size in addition to body weight and does not necessitate sacrificing individuals to determine relative condition levels. Several indices, using body weight in association with various structural parameters, have recently been used (Anderson 1972 for upland game birds, Bailey 1979 and Wishart 1979 for waterfowl, and Slagsvold 1982 for corvids). Brood patch development of some live-trapped gulls was subjectively assessed (large or small) according to size, amount of vascularization, and refeathering during the first week of incubation when the patch is fully developed in gulls (Paludin 1951).

Incubation behavior of 36 earlier and 5 later nesting pairs visible from a blind, was monitored by recording behavior of the birds every 3 min for one hour each in the morning, afternoon, and evening (point sample method, Dunbar 1976). The behavior of each bird was recorded as incubating (sitting on eggs), "settling," "waggling," or "sideways building" (Beer 1961, 1963). The latter 3 behaviors were lumped as "restless" because we did not think they represented those during which optimum heat transfer occurred between the attending bird and the eggs (Drent et al. 1970).

Statistical treatments followed Nie et al. (1975). Student's *t*-test was used when variances, tested by one-way ANOVA, were not significantly different at the 5% level. The Mann-Whitney *U*-test was used with small unequal samples because this test is not affected by extreme values (Zar 1974). In all cases significance is assumed at the 5% level.

RESULTS

The reproductive performance of earlier and later nesting gulls is summarized in Table 1. It is clear that earlier birds laid proportionately more and larger eggs which produced more fledged young than later

TABLE 1. Reproductive performance of earlier and later nesting Ring-billed Gulls, Granite Island, 1979.

	Early	Late	P (t-test*, χ^2**)
Clutch size	2.9 ± 0.5 (67)[a]	1.8 ± 0.8 (109)	<0.05*
Egg size			
Length (mm)	59.1 ± 2.2 (218)[b]	58.6 ± 2.5 (192)	<0.05*
Breadth (mm)	42.2 ± 1.2 (218)	41.3 ± 1.2 (192)	<0.05*
Volume (cc)	51.6 ± 3.7 (218)	48.9 ± 3.6 (192)	<0.05*
Hatching success[c]	73.2 (220)	16.1 (192)	<0.05**
Fledging success[d]	69.6 (161)	38.7 (31)	<0.05**
Incubation behavior			
% time on nest	97.8 (11,438/11,698) (36)[e]	95.6 (1637/1713) (5)	
% time "restless"	2.3 (260/11,438) (36)	4.6 (76/1637) (5)	<0.05** <0.05**

[a] x̄ ± SD (no. nests in sample).
[b] x̄ ± SD (no. eggs in sample).
[c] % of eggs laid that hatched (Burger 1979).
[d] % of eggs hatched that survived to 21 days (Gilman et al. 1977).
[e] (No. of observations in each category/total no. of observations) (no. nests in sample area), see text.

pairs. The nutrient composition of egg yolks differed very little (Table 2). The only apparent differences were in the greater dry weights of albumen and shell, reflecting, in view of the similar dry yolk weights, the larger average egg size of the earlier nesting birds (Table 1).

TABLE 2. Egg components and nutrient composition of yolk in freshly laid eggs of earlier and later started nests of Ring-billed Gulls, Granite Island, 1979.

	Earlier	Later	P (t-test)
Yolk			
Wet weight (g)	17.3 ± 2.4 (8)[a]	16.3 ± 1.5 (8)	NS
Dry weight (g)	7.2 ± 0.7 (21)	7.1 ± 0.5 (17)	NS
% Lipid	72.6 (20)	70.1 (19)	NS
% Nitrogen	27.4 (15)	29.9 (18)	NS
Albumen			
Dry weight (g)	4.2 ± 0.4 (33)	3.9 ± 0.4 (18)	<0.05
Eggshell			
Dry weight (g)	3.6 ± 0.3 (31)	3.3 ± 0.3 (18)	<0.05
Thickness (mm)	0.3 ± 0.02 (33)	0.3 ± 0.02 (20)	NS

[a] x̄ ± SD (no. eggs in sample). Sample sizes vary because not all measurements were taken from all eggs in clutches (see text).

TABLE 3. Body weight and condition index of earlier and later nesting Ring-billed Gulls, Granite Island, 1979.

	Earlier	Later	*P* (Mann-Whitney *U*-test)
Body weight[a]			
Males	601.5 (530–650) 8[b]	550.0 (430–590) 10	<0.05
Females	506.0 (470–555) 5	463 (405–530) 12	<0.05
Condition index			
Males	4.4 (4.2–4.9) 7	4.1 (4.1–4.2) 3	<0.05
Females	4.3 (4.1–4.7) 3	3.7 (3.3–4.2) 7	<0.05

[a] Sample sizes vary because not all captured birds were measured in an effort to reduce disturbance in the colony.
[b] Median (range) sample size.

Incubation attentiveness (% time sitting) was high in both groups (Table 1). The calculated significant differences may have little biological meaning in terms of the care and development of the eggs because the incubation periods for earlier and later eggs (26.1 ± 1.9 days, n = 142 vs. 25.9 ± 1.9 days, n = 29 respectively) were not significantly different (Mann-Whitney *U*-test = 1.96). The major differences seen between the groups during the incubation period were in the nest desertion rate and development of the brood patches. Thirty-one of 109 (28.4%) later nesting pairs deserted their nests relative to only 3 of 72 (4.2%) earlier nesting pairs ($\chi^2 = 16.7$, $P < .05$). Additionally, 9 of 11 (82%) earlier birds, captured during their first week of incubation, had large, well-vascularized brood patches that showed little evidence of refeathering. Only 4 of 21 (19%) later nesting gulls had large well-vascularized patches without any refeathering during their first week of incubation. The differences in development are significant ($\chi^2 = 11.8$, $P < .05$).

Body weights and condition index results are presented in Table 3. Because of the small sample size of birds from which we were able to obtain all measurements, we used the Mann-Whitney *U*-test to determine significance between the median body weights and condition index (Sokal and Rohlf 1981). The results show that males were heavier than females in both groups ($P < .05$) and that earlier nesting birds were in better condition than their later nesting counterparts.

DISCUSSION

The differences in reproductive performance of earlier and later nesting gulls agree with the results of other studies of colonial nesting seabirds (see Ryder 1980 for review). The relative body weight and condition index differences suggest that earlier nesting birds entered the nesting period with sufficient nutrient reserves to allow them to lay more and larger eggs, that contained about 8% more albumen, than individuals that delayed nest and clutch initiation. Whether the overall 8% difference in albumen has any real importance to embryonic and chick survival is unknown because the critical amount of albumen required for normal development in wild birds has not been documented. Nisbet (1978) suggests however, that the larger amounts of albumen he found in larger eggs of Common Terns (*Sterna hirundo*) (see also Parsons 1976, Ricklefs 1977, Jones 1979) may be critical to the survival of young during the first few days after hatching. It contains about two-thirds of the protein available for the developing embryo and it likely becomes an important agent involved in providing the young with sufficient vigor for food acquisition.

Why some birds delay their nesting activities is enigmatic. It might well be related to their relative foraging efficiency or effort (Pugesek, in press) and consequent storage of the required amounts of body reserves (fats and proteins) while en route north from their wintering areas. The gulls that nest on Granite Island usually arrive each year in the Black Bay area about the middle to latter part of April, although young birds might arrive later (Coulson 1966). Here they forage at the mouths of small rivers for spawning rainbow smelt (*Osmerus mordax*). It is conceivable that gulls that are more efficient or diligent in catching smelt might reach optimum breeding condition earlier than gulls less successful at capturing these small fish. This latter group may not be able to accumulate the necessary amount of nutrients before entering the nesting season. This may be manifest in their lighter body weights (Young and Boag 1982), smaller clutches and eggs (Coulson et al. 1982), their propensity to desert their nests (see Ankney and MacInnes 1978), and their inability to produce normal-sized and well-vascularized brood patches (Follet 1973).

We have some evidence that suggests proportionately more young gulls nest later in the season. Of 11 earlier nesters captured during incubation, 2 (18%) were in immature plumage (Ryder 1975), whereas 10 of 28 (36%) later nesters were in immature plumage during incubation. That younger gulls are usually less successful foragers (Tolonen 1976) and typically nest later (Ryder 1980) than older individuals is well known. It thus appears the results of this study are, in part, explained by an age differential between the earlier and later nesting pairs and that timing of nesting and reproductive performance might be proximally based on body condition (nutritive status, Young and Boag 1982) attained just before the time and place of nesting.

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