EGG-LAYING, EGG SIZE, AND SUCCESS IN RELATION TO IMMATURE-MATURE PLUMAGE OF RING-BILLED GULLS

JOHN P. RYDER

Important direct relationships between the age of parents and their success at hatching eggs and rearing young are known for the Kittiwake (*Rissa tridactyla*) (Coulson and White 1958), Herring Gull (*Larus argentatus*) (Parsons 1971), and Red-billed Gull (*L. novaehollandiae*) (Mills 1973). Additionally, egg size, calculated from length and width (Stonehouse 1966) correlates positively with hatchability of Shag (*Phalacrocorax aristotelis*) eggs (Coulson et al. 1969) and survival of young Herring Gulls (Parsons 1970). The relation between age and egg size, wherein older birds lay larger eggs than younger ones, has been noted in the Shag (Coulson et al. 1969), Kittiwake (Coulson 1963), Gannet (*Sula bassana*) (Nelson 1966), and Short-tailed Shearwater (*Puffinus tenuirostris*) (Serventy 1967). Coulson (1963) found the latter relationship useful for estimating age composition of Kittiwake populations.

Investigations on age-specific breeding biology have relied on large samples of banded birds secured over many years. These long term banding operations to secure a sample of known-aged birds, potentially delay research which is dependent on some knowledge of the age composition of a population. In any initial study of a species it is of considerable value if a field method is available which can be used to estimate the variance in age and experience of members of a breeding population.

I have noted that nesting pairs of Ring-billed Gulls (*L. delawarensis*) can be separated into 3 categories based on plumage characteristics. Most pairs on my study area consisted of 2 birds in mature plumage. The head, body, wing linings, body feathers, and rectrices of such individuals were typically white, and the 6 outer primaries each had a distal white spot or window. Other pairs consisted of one bird in mature plumage and one in immature plumage. Some pairs were formed of 2 birds with immature plumage. Immature plumage in Ring-billed Gulls is characterized by the absence of white spots on the primaries, brown-edged wing coverts, a sub-terminal black band or spots on the rectrices, and black-tipped head feathers (Ludwig 1974).

Based on these observations, I considered whether the breeding biology of the 3 pair-types reflected age-specific differences in laying dates, clutch size, egg size, and success that have been reported from other larids of known age.

In this study I assumed that birds in immature plumage are younger and have less breeding experience than birds in mature plumage. Ludwig (1974) reported that 75% of banded Ring-billed Gulls recovered in cannon nets on a breeding colony averaged 3.27 years and were in adult plumage. Over 65% of those gulls which averaged 2 years of age were in immature plumage, of which 33% attempted to breed for the first time. Although precise ages cannot be determined in Ring-billed Gulls on the basis of plumage characteristics (Ludwig 1974), relative ages can be assigned.

METHODS

In 1973, I obtained 159 Ring-billed Gull nest histories from a colony of approximately 800 pairs on Granite Island (48°43′ N, 88°29′ W), Black Bay, northern Lake Superior, Ontario. Of the 159 nests, 118 were each attended by 2 gulls in mature plumage. Thirty-four nests were each attended by one mature-plumaged bird and one immature-plumaged bird. Seven nests were attended by 2 immature-plumaged birds. The 3 pair types are designated here as A × A, A × B, and B × B; A indicating a mature-plumaged bird, and B an immature-plumaged bird. I noted from copulatory behavior that the immature-plumaged bird of each A × B pair was male. Mills (1973) found the male was the younger member of a pair in 57% of 212 pairs of Red-billed Gulls. He attributed this to lower survival of males. Possibly a similar situation occurs in Ring-billed Gulls. It might also indicate that males breed when younger than females or that females acquire mature plumage at an earlier age.

I watched Ring-billed Gull nests daily from an observation tower adjacent to the nesting colony. New eggs were marked in sequence in each clutch. Length and maximum breadth of eggs were obtained for 55 A × A clutches, 22 A × B clutches and 5 B × B clutches. Ten 3-egg clutches were collected and egg volume determined to the closest 0.1 cm^3. Using these data I was then able to estimate volume of uncollected eggs by the method described in Coulson (1963). The formula I used to estimate volume was: $V = 0.489 \times B^2 \text{ (max)} \times L$, where B is the maximum breadth and L the length of each egg. Recently Preston (1974) questioned this method of calculating absolute egg volumes because the equation does not incorporate enough data. However, in this paper, I am not so much interested in the absolute volume as much as relative egg volumes of the 3 pair types. Preston (pers. comm.) found only about a 2% difference in Ring-billed Gull egg volumes calculated by his method as compared to the above equation.

RESULTS

Clutch initiation.—A × A pairs began clutches 2 weeks earlier (first week of May) than A × B pairs. B × B pairs started latest, during the fourth week of May (Fig. 1). The median dates of egg-laying (the day by which 50% of the pairs had begun their clutches) for the A × A, A × B, and B × B pairs were 18, 26, and 30 May respectively.

Clutch size.—Table 1 shows a seasonal reduction in average clutch size in each of the pair types. The proportions of 1, 2, and 3-egg clutches are similar in A × A and A × B pairs (Table 2). Data for B × B pairs are too few to consider further. Clutches of 5 eggs or more might represent those laid by

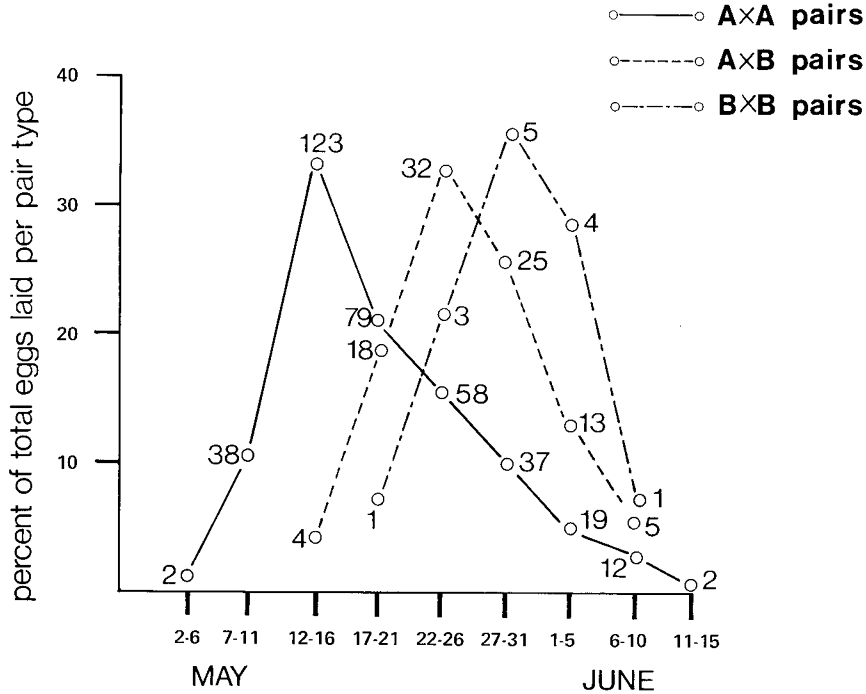

FIG. 1. Number of eggs laid per week by A × A, A × B, and B × B pairs of Ring-billed Gulls, Granite Island, 1973. Numbers on Figure are eggs laid per week.

more than one female as was suggested for the Ring-billed Gull by Vermeer (1970). If the 5, 6, and 7-egg clutches are deleted from Table 1, the means for A × A and A × B pairs are 2.86 ± 0.63 and 2.79 ± 0.48 ($P > 0.05$) respectively.

Hatching success was greatest in 3-egg clutches (Table 2). Similar variation has been found in Herring Gulls, Lesser Black-backed Gulls (*L. fuscus*), Great Black-backed Gulls (*L. marinus*), and Western Gulls (*L. occidentalis*) (Paynter 1949, Harris 1964, Hunt and Hunt 1973).

Egg-size characteristics.—Table 3 summarizes egg size parameters of each pair type. Significant differences in mean length ($P < 0.05$) occurred between first and second, and first and third eggs of A × A pairs. The first and second eggs of A × A and A × B pairs had a similar breadth ($P > 0.05$) but third eggs in these 2 groups were narrower and had less volume ($P < 0.05$) than first or second eggs. The shape index (100 × breadth/length) (Coulson 1963) of A × A second eggs was larger than first or third eggs, indicating that egg was slightly shorter and wider. Between the A × A and

TABLE 1
CLUTCH SIZE OF MARKED RING-BILLED GULL NESTS ON GRANITE ISLAND, 1973

Week of clutch initiation	Average clutch size		
	A × A	A × B	B × B
2–6 May	6.00 (1)	—	—
7–11 May	3.76 ± 0.83* (17)	—	—
12–16 May	3.49 ± 1.08 (43)	3.67 (3)	—
17–21 May	3.20 ± 1.32 (20)	3.00 ± 0.54 (8)	3.00 (1)
22–26 May	2.61 ± 0.61 (18)	3.00 ± 0.60 (12)	2.00 (1)
27–31 May	1.86 ± 0.69 (7)	2.75 (4)	2.00 (2)
1–5 June	2.29 ± 0.95 (7)	2.20 ± 0.84 (5)	1.67 (3)
6–10 June	2.00 ± 0.71 (5)	2.00 (2)	—
Total	3.14 ± 1.16 (118)	2.85 ± 0.78 (34)	2.00 ± 0.82 (7)

* Standard deviation of the mean (also in Tables 3, 4, and 5).

A × B pairs the only significant difference in any of the parameters was the mean breadth of the third egg. Although my sample size of B × B eggs is too small for statistical comparisons, the means of the parameters show all these eggs were smaller than eggs of the other pair types. Shape index values indicate B × B eggs were shorter and broader than their A × A and A × B counterparts.

For all parameters, successful eggs were numerically, but not significantly, larger than unsuccessful eggs (Table 4). Both successful and unsuccessful eggs of A × A pairs averaged larger than eggs of A × B pairs.

Mature-plumaged pairs which started their clutches on or before the mean date of clutch initiation (17 May) laid larger eggs than pairs which started their clutches after the mean date (Table 5). A similar trend occurred in A × B and B × B pairs. Only differences in egg volumes of early and late starting A × A pairs reach significance.

The differences in the median dates of laying among the 3 groups are reflected in their respective success rates. Eggs laid by mature-plumaged pairs had a hatching success approximately twice that of eggs laid by pairs with one immature-plumaged bird. All eggs of B × B pairs were destroyed by a predator, probably Common Crows (*Corvus brachyrhynchos*), within 2 days after laying of the complete clutch. A × B pairs lost 80% of their eggs to predators.

TABLE 2

CLUTCH SIZE FREQUENCY AND HATCHING SUCCESS OF EGGS IN MARKED RING-BILLED GULL NESTS, GRANITE ISLAND, 1973

Clutch size	A × A		A × B		B × B	
	number	H.S.[1]	number	H.S.	number	H.S.
1	7 (5.9)[2]	14.2 (1/7)	2 (5.9)	0.0 (0/2)	2 (28.6)	0.0 (0/2)
2	21 (17.8)	16.7 (7/42)	6 (17.6)	0.0 (0/12)	3 (42.9)	0.0 (0/6)
3	59 (50.0)	62.7 (111/177)	22 (64.7)	31.8 (21/66)	2 (28.6)	0.0 (0/6)
4	20 (16.9)	48.9 (39/80)	3 (8.8)	0.0 (0/12)	—	—
5	3 (2.5)	20.0 (3/15)	1 (2.9)	0.0 (0/5)	—	—
6	7 (5.9)	14.3 (6/42)	—	—	—	—
7	1 (0.9)	0.0 (0/7)	—	—	—	—
Means	3.14 ± 1.16 (118)	45.1 (167/370)	2.85 ± 0.78 (34)	21.6 (21/97)	2.00 ± 0.82 (7)	0.0 (0/14)

[1] H.S. = hatching success (number of eggs hatched/number laid).
[2] percent of total clutches.

TABLE 3
MEAN LENGTH, BREADTH, VOLUME, AND SHAPE INDEX OF RING-BILLED GULL EGGS, GRANITE ISLAND, 1973

	A × A	A × B	B × B
Length (mm)			
1st egg	60.94 ± 2.88 (55)[1]	59.43 ± 3.23 (22)	56.88 ± 3.27 (5)
2nd egg	59.51 ± 2.23 (55)	59.48 ± 2.75 (22)	55.44 ± 2.04 (4)
3rd egg	59.25 ± 2.60 (55)	59.18 ± 1.93 (22)	57.12 ± 0.95 (2)
Mean	59.90 ± 2.09 (55)	59.36 ± 2.26 (22)	55.85 ± 3.14 (5)
Breadth (mm)			
1st egg	41.94 ± 1.31	42.06 ± 1.38	40.57 ± 0.95
2nd egg	42.31 ± 1.09	41.89 ± 1.18	41.24 ± 0.61
3rd egg	41.83 ± 1.38	41.17 ± 0.94	40.40 ± 0.28
Mean	42.02 ± 1.08	41.70 ± 0.81	40.78 ± 0.78
Volume (cm^3)			
1st egg	52.51 ± 4.37	51.42 ± 3.70	45.83 ± 3.96
2nd egg	52.15 ± 3.51	51.15 ± 4.31	46.13 ± 2.74
3rd egg	50.79 ± 4.35	49.11 ± 3.21	45.58 ± 0.13
Mean	51.81 ± 3.57	50.54 ± 3.02	45.89 ± 2.92
Shape Index			
1st egg	68.96 ± 3.58	71.01 ± 5.27	71.49 ± 4.00
2nd egg	71.19 ± 3.08	70.54 ± 3.08	74.44 ± 2.29
3rd egg	70.71 ± 3.46	69.61 ± 2.06	70.74 ± 1.68
Mean	70.23 ± 2.57	70.34 ± 2.81	72.43 ± 3.29

[1] Number in parentheses is clutch sample size.

DISCUSSION

The overriding trends found in this study were that pairs of Ring-billed Gulls which contained at least one immature-plumaged individual started their nesting activities later in the season and laid smaller eggs which were less likely to hatch than pairs composed of 2 mature-plumaged gulls. The reason for the above differences in Ring-billed Gull biology is unknown (but see Perrins 1970:248). Mills (1973) suggested from his work on Red-billed Gulls that slower maturation of the testes of the young gulls delayed courtship and nesting activities. Pairs with 1 or 2 immature-plumaged Ring-billed Gulls seem to spend more time establishing territories. Though territorial behavior was not studied in detail, I noted that 62% of A × B and B × B pairs nested on the periphery of the Granite Island colony. A similar distribution of Ring-billed Gulls, according to age, was noted by Ludwig (1974). Possibly by the time immature birds are physiologically and behaviorally ready to breed, sites

TABLE 4
MEAN LENGTH, BREADTH, VOLUME, AND SHAPE INDEX OF SUCCESSFUL AND UNSUCCESSFUL RING-BILLED GULL EGGS, GRANITE ISLAND, 1973

	Successful eggs	Unsuccessful eggs
Length (mm)		
A × A	60.06 ± 2.54 (107)	59.59 ± 2.91 (58)
A × B	59.51 ± 3.00 (21)	59.29 ± 2.52 (45)
Breadth (mm)		
A × A	42.16 ± 1.14	41.77 ± 1.47
A × B	41.79 ± 0.81	41.66 ± 1.38
Volume (cm^3)		
A × A	52.26 ± 3.00	50.99 ± 5.08
A × B	50.88 ± 3.63	50.41 ± 4.00
Shape Index		
A × A	70.33 ± 3.63	70.21 ± 3.26
A × B	70.37 ± 3.40	70.40 ± 3.88

in the center of the colony are filled by adults. Adults may also actively exclude younger birds from the center.

The differences in egg success between mature-plumaged and immature-plumaged pairs can most readily be explained by behavioral differences. I have observed in the Granite Island colony that the most persistant incubators are mature-plumaged pairs. If we accept Drent (1973:294) that experience is interwoven with age, then the smaller eggs of immature-plumaged gulls are likely more susceptible to predation than eggs attended by older birds. My observations on the A × B and B × B pairs suggest that egg predation is an important factor governing success of these groups.

These results generally follow the findings of other workers who have investigated age-specific breeding biology of known-age larids. Of significance is that age-specific differences can be demonstrated from plumage differences in Ring-billed Gulls.

SUMMARY

Nesting pairs of Ring-billed Gulls were visually separated into 3 pair types, based on the plumage of mated individuals. Pairs consisted of either 2 mature-plumaged birds, one mature-plumaged bird and one immature-plumaged bird, or 2 immature-plumaged birds. Aspects of the breeding biology confirmed that mature-plumaged pairs nested earlier, had larger clutches and larger eggs which were more successful than pairs with one or more immature-plumaged individuals.

TABLE 5

MEAN LENGTH, BREADTH, VOLUME, AND SHAPE INDEX OF EARLY AND LATE STARTED RING-BILLED GULL CLUTCHES, GRANITE ISLAND, 1973

	Early-started clutches[1]	Late-started clutches[2]
Length (mm)		
A × A	60.07 ± 2.33 (29)	59.70 ± 1.82 (26)
A × B	59.94 ± 2.20 (11)	58.79 ± 2.27 (11)
B × B	57.65 ± 2.10 (3)	54.20 ± 1.38 (2)
Breadth (mm)		
A × A	42.37 ± 0.94	41.65 ± 1.11
A × B	41.88 ± 0.56	41.53 ± 0.99
B × B	40.71 ± 0.94	40.90 ± 0.50
Volume (cm^3)		
A × A	52.77 ± 3.14	50.73 ± 3.78
A × B	51.45 ± 2.80	49.62 ± 3.07
B × B	46.77 ± 3.33	44.37 ± 1.26
Shape index		
A × A	70.63 ± 3.09	69.78 ± 1.78
A × B	69.94 ± 2.22	70.75 ± 3.36
B × B	70.66 ± 2.33	75.51 ± 2.36

[1] Early-started clutches are those started on or before May 17 for A × A pairs, May 25 for A × B pairs, and May 29 for B × B pairs.

[2] Late-started clutches were begun after May 17 by A × A pairs, May 25 for A × B pairs, and May 29 for B × B pairs.

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DEPT. OF BIOLOGY, LAKEHEAD UNIV., THUNDER BAY, ONTARIO, CANADA, P7B 5E1.
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NEW LIFE MEMBER

Dr. Thomas C. Dunstan is now a life member of the Wilson Ornithological Society. He is presently Assistant Professor of Biology at Western Illinois University, Macomb, Illinois. Dr. Dunstan's professional interests include radio-telemetry studies on raptorial birds, and he has published a number of papers dealing with Bald Eagles, Ospreys, and Great Horned Owls as well as other raptors. Dr. Dunstan is married and has two children. In addition to his ornithological interests Dr. Dunstan enjoys photography, crosscountry skiing, wilderness camping, and canoeing.