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# CHARACTERISTICS OF SUPERNORMAL RING-BILLED GULL CLUTCHES AND THEIR ATTENDING ADULTS

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Recent reports of female-female pairing and/or polygyny in Western Gulls (*Larus occidentalis*) (Hunt and Hunt 1977), Ring-billed Gulls (*L. delawarensis*) (Conover et al. 1979a, Ryder and Somppi 1979), California Gulls (*L. californicus*) (Conover et al. 1979a), and Herring Gulls (*L. argentatus*) (Shugart and Southern 1977, Fitch 1979, Shugart 1980), indicate plasticity in the mating systems of larids. Such plasticity may allow individuals to adjust to changing ecological constraints. Certain behaviors are adaptive in one situation but not another and mating systems of local populations of the same species may vary in different environmental or density situations (Emlen and Oring 1977).

In mate selection, any given female will choose from the subset of available mates she contacts during the appropriate, critical time period (Gladstone 1979). If a female recruit, "divorcee," or recent "widow" does not encounter any available territory-holding males, or cannot satisfactorily compete with older, more experienced, or more dominant females, she may be excluded from forming a heterosexual pair-bond. However, extra-pair copulations have been observed in gulls (Goethe 1937, Hunt and Hunt 1977, Conover et al. 1979a), thus providing an alternative possibility for unmated females. The recipient of an extra-pair copulation (i.e., the female) needs assistance to provide adequate parental care and to minimize her energy expenditure. Females who co-operate and form an association with another female increase their reproductive experience (if they can find space to nest) and increase their fitness if young are raised. This would be adaptive under ecological conditions which bias the operational sex ratio (the ratio of sexually active males to fertilizable females [Emlen and Oring 1977]) in favor of females.

In recent years there has been a very marked expansion in the range and numbers of the Ring-billed Gull (Ludwig 1974, Conover et al. 1979b). It is in areas of range expansion and growing colonies that supernormal clutches ($N \geq 5$ eggs) now occur. Supernormal clutches are frequently attended by two females (Conover et al. 1979a, Ryder and Somppi 1979, Kovacs-Nunan 1982) suggesting anomalies in the operational sex ratio. Such anomalies in the sex ratio have been documented in the Western Gull and Herring Gull (Burger and Gochfeld 1981). In this paper we report the incidence, composition and fertility of supernormal Ring-billed Gull

clutches in a large, relatively stable colony, and the sex and plumage characteristics of attending adults.

## METHODS

Supernormal (five- and six-egg) clutches observed in a colony of approximately 27,500 pairs (Blokpoel 1977, pers. comm.) on Gull Island, near Brighton, Ontario (43°50′N, 77°40′W), were marked with wooden stakes on 6 May 1980. Additional supernormal clutches were marked when found. In the course of our studies, the island was searched thoroughly and repeatedly, thus, the chances of our having missed any clutches are minimal. An attempt was made to trap attending adults at the nest, using the drop trap of Mills and Ryder (1979). All trapped individuals were banded with a USFWS aluminum band. Trapping efforts stopped when we captured two individuals from any one site; thus, we unfortunately did not allow for the possibility of a third attending bird (and hence the possibility of polygyny). However, we did check for the presence of unbanded individuals whenever we approached these nests and none were observed. Birds were sexed by bill measurements (Ryder 1978) and four individuals (two pairs) were collected to confirm the predicted sex by gonadal inspection. We classified each bird into one of two plumage types. It was considered a subadult if it possessed a subterminal tail-band or remnants thereof, buffy wing coverts, or had less than two white "windows" on the primaries. Adults were as described by Ludwig (1974). We have rarely observed gulls with a subterminal tail-band as well as "windows" in their primaries.

The length and maximum width of eggs were measured with vernier calipers. Eggs were opened near the end of the incubation period, checked for visible embryonic development, and the approximate age of the embryos recorded (Ryder and Somppi 1977). Obvious differences in background color and/or size of eggs within a clutch were recorded as an indication of the possibility that two females had contributed to the clutch, as there is generally a greater variability in egg size and background color among different Herring Gull clutches than within the same clutch (Baerends and Hogan-Warburg 1982). Where possible the supernormal clutches were subdivided into constituent clutches on the basis of similarity of background coloration and/or size. Eggs missing at the time of measuring were classified as of "unknown" fertility. In 1979, we trapped the attending adults on five supernormal clutches and opened the eggs.

## RESULTS

Twenty-one supernormal clutches (0.08%, based on an estimated population of 27,500 pairs) were found on Gull Island, Lake Ontario, in 1980. Embryonic age determinations suggested the majority (74%) were completed during the last week in April and the first week of May, corresponding to what appeared to be the peak of clutch completions in the colony.

In 14 of 21 supernormal clutches (66.6%) there were obvious differences in egg background color and/or size (Table 1). At five of these nests we were able to trap only one individual; thus, the sex of only 37 attending adults was determined. Eight (38.1%) of the supernormal clutches were attended by a male and at least one female. In three of these eight clutches there were differences in coloration and/or size suggesting the possibility of more than one female contributor (i.e., polygyny or nest parasitism)

TABLE 1

SEX AND PLUMAGE CHARACTERISTICS OF RING-BILLED GULLS TRAPPED ON SUPERNORMAL CLUTCHES, GULL ISLAND, 1980, IN RELATION TO CLUTCH-SIZE AND APPARENT FERTILITY

| Nest | Clutch composition[a] | Fertility[b] | Sex | Plumage type |
|---|---|---|---|---|
| 1 | 2 + 3 | 2 + 3 | M, F | Ad, Ad |
| 2 | 2 + 3 | 2 + 3 | M, F | Ad, Ad |
| 3 | 5 | 3 + 2U | M, F | Ad, Ad |
| 4 | 2 + 3 | 5 | M, F | Ad, Ad |
| 5 | 5 | 5 | M, F | SAd, SAd |
| 6 | 5 | 5 | M, F | Ad, Ad |
| 7 | 5 | 5 | M, F | SAd, SAd |
| 8 | 6 | 5 + 1U<br>38F, 3U (92.7%)[c] | M, F | Ad, Ad |
| 9 | 4 + 1 | (3 + 1U) + 1 | F, F | Ad, SAd |
| 10 | 2 + 3 | 2 + (2 + 1U) | F, F | SAd, SAd |
| 11 | 2 + 3 | 2 + 3 | F, F | Ad, SAd |
| 12 | 2 + 3 | (2 + 1I)(1 + 1I) | F, F | Ad, SAd |
| 13 | 6 | 3 + 2I + 1U | F, F | Ad, SAd |
| 14 | 3 + 3 | 3 + (2 + 1I) | F, F | Ad, SAd |
| 15 | 3 + 3 | 3I + 3I | F, F | Ad, Ad |
| 16 | 3 + 3 | 3 + 3I<br>27F, 14I, 3U (61%) | F, F | Ad, SAd |
| 17 | 2 + 3 | (1 + 1U) + (2 + 1I) | F, —[d] | Ad, — |
| 18 | 5 | 5 | F, — | Ad, — |
| 19 | 2 + 3[e] | (1 + 2U) + (2 + 1I) | F, — | Ad, — |
| 20 | 3 + 3 | 3 + 3 | F, — | Ad, — |
| 21 | 3 + 3[e] | (2 + 1U)(1 + 2U)<br>20, 2I, 6U (71%) | F, — | Ad, — |

[a] Grouping of eggs based on differences in coloration and/or measurements.
[b] Eggs are fertile unless noted otherwise: I = infertile, U = unknown.
[c] Total fertile (F), infertile (I) and unknown (U) (minimum fertility).
[d] Failed to trap "mate."
[e] One egg missing; given fate U.

(Table 1). We trapped two females at eight and single females at the remaining five supernormal clutches (Table 1) in contrast to a total of 25 males and 15 females trapped at 40 three-egg clutches in this colony during the same period ($\chi^2 = 13.115$, df = 1, $P < 0.001$). All five individuals trapped on supernormal clutches in this colony in 1979 were females in contrast to 11 of 20 attending two- and three-egg clutches ($P < 0.01$, Fisher's Exact Probability Test).

On the basis of our criteria six of eight of the heterosexual associations were comprised of individuals in adult plumage. In one instance two females attending a supernormal clutch were in adult plumage (Table 1). In

six others, one female was adult and the other subadult, and in one instance both females were in subadult plumage (Table 1). The difference in frequency of pairs with both plumage types between heterosexual associations and apparent female-female associations is significant ($P < 0.03$, Fisher's Exact Probability Test).

Based on eggs with embryonic development (minimum fertility estimate), supernormal clutches with a male in attendance had a higher minimum fertility (92.7%) than those at which no male was trapped (65.3%) ($\chi^2 = 18.53$, df = 1, $P < 0.001$) (Table 1). Of 25 eggs examined from supernormal clutches in this colony in 1979, a minimum of 16 (64%) was fertile and a minimum of five (20%) was infertile.

On 20 May 1980, a female (765–99332) in adult plumage attending a clutch of five eggs (3 + 2) was trapped on Gull Island. Another female (765–99335) was trapped on the same clutch on 24 May. Two eggs were infertile and the remainder addled. The nest was deserted by 27 May. On 12 June 1980, female 765–99332 was trapped on a clutch of four eggs (2 + 2) in the colony on the Eastern Headland, Toronto Outer Harbour (43°30′N, 79°22′W). Her "mate" was unbanded and could not be trapped but appeared to be a female (P. M. Fetterolf, G. Tessier, and H. Blokpoel, pers. comm.). Hence, female 765–99332 was a member of two distinct cooperative nesting associations in a single season, separated temporally by a maximum of 23 days and spatially by a distance of 142 km.

## DISCUSSION

Supernormal clutches have been mentioned in the Ring-billed Gull literature as early as 1941 and apparently occur throughout much of its present range (Table 2). The majority of supernormal clutches in this study were produced during the peak of egg-laying suggesting that they were not the result of "last resort" reproductive attempts nor that the behaviors by which they arose are only adopted by those females who arrive after the peak of clutch completion or who lose their mate after laying. Kovacs and Ryder (1981) have recently reported that some female-female associations are maintained for two successive years and that they show nest-site fidelity. Supernormal clutches are frequently attended by two females (this study, Conover et al. 1979a, Ryder and Somppi 1979) and in our study 50% of these females were in subadult plumage. If these subadult-plumaged females are indeed younger, they can increase their reproductive experience as a member of a female-female association and may thus enhance reproductive success in subsequent years. One female was a member of two female-female associations separated temporally and spatially within one breeding season.

Conover et al. (1979a) reported a polygynous group of three females and

TABLE 2

VARIATION IN CALCULATED PREVALENCE OF FIVE- AND SIX-EGG RING-BILLED GULL CLUTCHES IN COLONIES WITH PORTION OF RANGE, GROWTH STATUS, SIZE, AND TIME

| Portion of range | Colony location | Growth | Year | Size | Prevalence per 1000 nests | Source[e] |
|---|---|---|---|---|---|---|
| Long established | Miquelon Lake, Alta. | STBL[a] | 1965 | 435 | 2.3 | (1) |
| | Lozinsky's Slough, Sask. | STBL | 1958 | 1200 | 1.7 | (2) |
| | Bachelor's Is., Man. | STBL | 1979 | 1596 | 5.6 | (3) |
| | Rogers City, L. Huron | STBL | 1979 | 8000 | 3.0 | (4) |
| | Mohawk Is., L. Erie | DECN[b] | 1972 | 1000 | 5.7 | (5) |
| | Muggs Is., L. Ont. | INCR[c] | 1972 | 2375 | 19.0 | (5) |
| | | SAT'D[d] | 1980 | 6069 | 0.5 | (6) |
| | Gull Island, L. Ont. | SAT'D | 1980 | 27,500 | 0.8 | (7) |
| | Ile de la Couvee, St. Lawrence R. | INCR | 1978 | 11,000 | 24.1 | (8) |
| | Eastern Headland, L. Ont. | INCR | 1980 | 68,000 | 1.0 | (6) |
| Expansion | Honey Lake, Calif. | INCR | 1941 | 75 | 26.7 | (9) |
| | | INCR | 1953 | 717 | 34.9 | (10) |
| | Banks Lake, Wash. | INCR | 1978 | 2700 | 16.1 | (11) |
| | Sprague Lake, Wash. | INCR | 1978 | 850 | 18.0 | (11) |
| | Potholes Reservoir, Wash. | DECN | 1978 | 11,000 | 1.9 | (11) |
| | Okanagan Lake, B.C. | INCR | 1972 | 98 | 122.4 | (12) |
| | Vrooman Is., L. Superior | INCR | 1979 | 167 | 305.4 | (13) |
| | Gravel Is., L. Superior | SAT'D | 1979 | 378 | 5.3 | (14) |
| | Granite Is., L. Superior | INCR | 1977 | 1600 | 121.0 | (15) |
| | | INCR | 1979 | 2400 | 41.0 | (16) |
| | | INCR | 1980 | 2699 | 28.0 | (16) |

[a] Stable.
[b] Declining.
[c] Increasing.
[d] Saturated.
[e] (1) Vermeer (1970); (2) G. A. Fox (unpubl.); (3) Koonz (1980); (4) Wm. Southern (pers. comm.); (5) R. D. Morris (pers. comm.); (6) P. M. Fetterolf, G. D. Tessier and H. Blokpoel (pers. comm.); (7) this study; (8) Lagrande and Mousseau (1981); (9) Moffitt (1942); (10) Johnston and Foster (1954); (11) Conover et al. (1979a, 1979b); (12) Merilees (1974); (13) Blokpoel et al. (1980); (14) J. P. Ryder (pers. comm.); (15) Somppi (1978); (16) Kovacs-Nunan (1982).

a single male attending a supernormal clutch in a single nest bowl. Hence, our male-attended supernormal clutches may represent the products of polygynous groups although we did not observe any unbanded individuals incubating these clutches during casual observations. The eggs differed in size and/or coloration in only 37% of the male-attended superclutches and five-egg clutches were more frequent than six (Table 1). This suggests that a single female may have produced some of these supernormal clutches. We know of no documentation of a female Ring-billed Gull laying five eggs. However, Parsons (1976) has shown that 79% of 102 pairs of Herring

Gulls in a continuous laying experiment laid five or more eggs. Nest parasitism, which would also artificially increase clutch-size, has been observed in Ring-billed Gulls (D. Boersma, unpubl.). However, this mechanism is more likely to account for four-egg clutches than five- or six-egg clutches since the latter imply multiple acts of parasitism.

Minimum fertility of supernormal clutches ranged from 61–93% depending whether or not a male was in attendance. Other investigations have reported minimum fertilities of 60–75% in supernormal clutches of this species attended by female-female associations (Conover et al. 1979a, Ryder and Somppi 1979). These fertility rates are relatively high and do not differ from the average hatching success of normal clutches. This may reflect the fact that individuals of this species frequently nest at very high densities which may provide increased opportunity for fertilization through extra-pair copulations.

No data on the relative philopatry of the sexes have been published for this species. In Herring Gulls, the male is the more philopatric sex (Chabrzyk and Coulson 1976). Thus, in new or rapidly growing colonies, the majority of the immigrants will be female and often young (Kadlec and Drury 1968). On this basis, we would predict, in areas of range expansion, a greater prevalence of female-female associations and polygyny in small growing colonies than in large, possibly saturated, or declining colonies where an abundance of both sexes might be expected. A review of the available data supports this hypothesis (Table 2). The prevalence in colonies in the long-established range (median = 2.65/1000) is markedly lower than in those in areas of range expansion (median = 28.0/1000, $U = 14$, $P < 0.01$). The prevalence in growing colonies (median = 27.35/1000) is significantly higher than that in stable colonies (median = 2.65/1000, $U = 4$, $P < 0.01$) and declining or saturated colonies (median = 1.9/1000, $U = 30$, $P < 0.01$). This suggests that Ring-billed Gull supernormal clutches result from behavioral responses to a skewed operational sex ratio accompanying range expansion and/or colonization.

## SUMMARY

Some Ring-billed Gull (*Larus delawarensis*) clutches of five and six eggs in the Gull Island colony in Lake Ontario in 1980 were attended by at least two females while others were attended by at least one male and one female. Since we did not ascertain whether or not a third individual was in attendance, we can only conclude that these supernormal clutches resulted from active female-female associations, polygyny, or from a single female. The female-female associations frequently involved one individual in subadult plumage. One female was a member of two consecutive female-female associations at two different colonies in the same breeding season. Minimum fertility of supernormal clutches was higher in those with a male in attendance. The prevalence of supernormal clutches is higher in growing colonies and in areas of range expansion than in saturated and declining colonies or in colonies

within the long-established range. This suggests that supernormal clutches result from behavioral responses to a skewed operational sex ratio that accompanies range expansion and colonization.

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## COLOR PLATE

The colorplate frontispiece of Bluish-slate Antshrike (*Thamnomanes schistogynus*) has been made possible by an endowment established by George Miksch Sutton (1898–1982). Painting by F. P. Bennett, Jr.