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FREQUENCY, SPATIAL DISTRIBUTION AND NEST ATTENDANTS OF SUPERNORMAL CLUTCHES IN RING-BILLED AND CALIFORNIA GULLS

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ABSTRACT.—This study examined the occurrence and cause of supernormal clutches (SNC; 4–6 eggs) in Ring-billed (*Larus delawarensis*) and California (*L. californicus*) gulls, species that normally lay two- to three-egg clutches. In Washington and Oregon, clutches of five to six eggs constituted 0.8% of the clutches in Ring-billed Gulls ($n = 20{,}353$) and 0.1% in California Gulls ($n = 6{,}117$) during the mid-incubation period. The frequency of supernormal clutches in Ring-billed Gulls varied significantly both among colonies and years on a region-wide basis but this was not true in California Gulls. The frequency of four-egg clutches was correlated with that of five- to six-egg clutches within each species, but no correlation existed between the two species. Multi-female associations were responsible for 30% of the examined four-egg clutches ($n = 20$) in Ring-billed Gulls and 27% of them ($n = 11$) in California Gulls. All examined clutches of five or six eggs in Ring-billed Gulls ($n = 11$) and California Gulls ($n = 1$) were incubated by multi-female associations. In Ring-billed Gulls, 79% of the detected multi-female associations were female-female pairs, 16% were polygynous groups, and one was a group of three females but no males. In California Gulls, for these clutches, only female-female pairs were detected.

Gulls normally lay clutches of one to three eggs but clutches of four to seven eggs are occasionally found. These unusually large or supernormal (Bonner 1964) clutches have attracted the attention of ornithologists for many years (Call 1891, Jones 1906, Willett 1919). Not until 1977, however, was it discovered that supernormal clutches (SNCs) are produced by female-female pairs in Western Gulls (*Larus occidentalis*; Hunt and Hunt 1977). Such pairs have since been found also attending SNCs in California Gulls (*L. californicus*; Conover et al. 1979a), Ring-billed Gulls (*L. delawarensis*; Conover et al. 1979a, Ryder and Somppi 1979) and Herring Gulls (*L. argentatus*; Fitch 1980, Shugart 1980). Some SNCs also result from polygyny (Conover et al. 1979a, Lagrenade and Mousseau 1983). Hereafter, I will refer collectively to these associations where two or more females lay eggs in the same nest and share parental responsibilities (polygyny, female-female pairings, or multi-female groups) as "multi-female associations" (MFAs).

It is unclear why female-female pairs or polygynous associations occur in gulls that are normally monogamous, but one hypothesis is that they result from a shortage of breeding males. Support for this hypothesis comes from the finding that females outnumbered males at a Western Gull colony where there was a high frequency of female-female pairs (Hunt et al. 1980). Conover and Hunt (1984) also showed that SNC frequencies increased in Ring-billed and California gull colonies after the breeding adult sex-ratios were skewed by removing breeding males. These findings, however, do not explain why a shortage of breeding males should exist in some gull populations. One hypothesis is that DDT can feminize male gull embryos so that these individuals do not breed as adults (Fry and Toone 1981). This hypothesis may explain the increase in SNC frequencies since the 1940s in Western Gulls breeding off the California coast (Hunt and Hunt 1977), in Herring Gulls breeding in the Great Lakes (Conover 1984), and in the United States population of Caspian Terns (*Sterna caspia*; Conover 1983). In most larids, however, SNC frequencies have not increased significantly in recent years (Conover 1984). Too little is yet known about proximate factors affecting SNC frequencies, or the variability of SNC frequencies, to understand the significance of these large increases in SNC frequencies. In this study, I examined variability in SNC frequencies by testing the hypotheses that within the same population: 1) SNC frequencies change during the incubation period and 2) their frequency varies both among years and colonies.

A major difficulty with studying female-female pairs or polygynous associations in gulls is identifying them. Sexual dimorphism is so slight in these birds that many individuals can be sexed only by head or bill measurements or by laparotomy. For this reason, nests containing SNCs are often used to identify female-

female pairings and counts of SNCs are used to estimate the frequency of female-female pairings in colonies or populations (Hunt and Hunt 1977, Conover et al. 1979a, Shugart 1980, Conover 1983, Kovacs and Ryder 1983). If most or all SNCs do result from female-female pairs or polygynous associations, then it should be possible to study these reproductive associations by examining the distribution and frequency of SNCs. In this study, I also tested this assumption by determining what proportion of SNCs resulted from female-female pairs and polygynous associations in Ring-billed and California gulls.

METHODS

My study was conducted during five breeding seasons from 1976–1981 at eight Ring-billed and nine California gull colonies located in the eastern half of Oregon and Washington; these colonies and their locations are described elsewhere (Conover et al. 1979b). No data were collected during 1981 on Ring-billed Gulls nesting at the Cabin Island colony and on California Gulls nesting at the Cabin Island, Potholes Reservoir, Little Memaloose, and Miller Rocks colonies because another experiment conducted that year may have influenced the frequency of SNCs there (Conover 1984). For colonies with fewer than 2,000 nests, I recorded the clutch size of all nests; for larger colonies, clutch size data were obtained by sampling all nests in the colony or in transects running through the colony.

I counted clutches in the middle of the incubation period from 12–22 May, surveying all but a few colonies from 13–18 May. SNCs were counted during the mid-incubation period because 1) their number and frequencies were highest during this time in the colonies under study and 2) their numbers were relatively stable during this period, allowing reliable comparisons between colonies and years.

Observations made over five years indicated that hatching peaked at approximately the same time in all colonies with the exception of the Sprague Lake colony, which was usually five to seven days behind the others. The peak hatching date also varied little among years. For all colonies that were repeatedly surveyed during the same year, I used the count made closest to 15 May, except for Sprague Lake, where I used the date closest to 20 May.

SEASONAL VARIABILITY IN SNC FREQUENCIES

For this portion of the study, clutch sizes were counted repeatedly during a single year at the Cabin Island, Potholes Reservoir, and Sprague Lake colonies. This information was then examined to determine how the frequency of SNCs changed during the incubation period. Large changes in SNC frequencies during the course of the incubation period would indicate that reliable comparisons of SNC frequencies among years or colonies could be made only if the counts were made at the same phase of the incubation period.

YEARLY AND LOCATIONAL VARIABILITY IN SNC FREQUENCIES

For each colony, I determined the frequency of Ring-billed and California gull SNCs during each year of observation. These data were then summed for each colony and tested with Chi-square to determine whether the frequency of SNCs varied significantly among colonies. The data for all colonies were then summed for each year and a Chi-square test conducted to assess differences in SNC frequencies among years. Because not every colony was sampled each year, an interaction effect could exist whereby variability among either years or colonies could affect the other. To minimize this problem, I also tested for significant differences among colonies by combining data from 1978 and 1981 (the two years when the most data were collected) and limited the analysis to those colonies sampled in both years. Further, I tested for significant differences among years by using the four years of data from the two colonies near Richland (Island 18 and Island 20). This experiment was intended to reveal whether local or seasonal conditions influence SNC frequencies.

I next tested the data using the Spearman rank correlation coefficient to see whether the frequency of four-egg clutches correlated with that of five- and six-egg clutches within each species, an expected result if some four-egg clutches were produced by MFAs. Additionally, I examined whether the frequencies of SNCs in Ring-billed and California gulls were correlated. This would occur if SNC frequencies in both species were influenced by the same local conditions. For this analysis, I excluded any data where fewer than 100 nests had been checked in a colony in any given year.

NEST ATTENDANTS

To determine the role of different multi-female associations in producing SNCs, I randomly selected nests of specific clutch sizes from all nests of that size at the Potholes Reservoir, Island 18, and Island 20 colonies during 1981. I then attempted to sex every bird attending these nests. Each nest was marked with a stake and all birds incubating these nests were marked by placing rhodamine dye in the nests. The resulting dye-marks and patterns allowed me to individually identify all nest attendants.

TABLE 1. Chronology of clutch sizes in Ring-billed and California gulls in Washington.

		Ring-billed Gull							California Gull						
		No. nests	Clutch size						No. nests	Clutch size					
Colony	Date		1	2	3	4	5	6		1	2	3	4	5	6
Cabin Island	4/28/81	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5/17/81	265	17	40	191	11	6	0	11	0	2	8	1	0	0
	6/2/81*	403	29	47	313	9	5	0	17	0	4	13	0	0	0
Potholes Reservoir	4/27/81	1,307	615	461	226	5	0	0	307	193	78	36	0	0	0
	5/4/81	2,918	508	718	1,628	62	1	1	905	179	225	494	7	0	0
	5/15/81	3,772	245	624	2,820	75	6	2	1,369	77	244	1,020	26	2	0
	5/18/81	–	–	–	–	–	5	2	–	–	–	–	–	2	0
	5/27/81*	3,040	285	761	1,950	39	5	0	977	52	255	654	15	1	0
Sprague Lake	4/27/77	1	1	0	0	0	0	0							
	4/30/77	28	18	10	0	0	0	0							
	5/4/77	258	126	88	43	1	0	0							
	5/7/77	501	123	159	215	4	0	0							
	5/12/77	838	44	141	637	7	7	2							
	5/15/77	899	37	90	754	10	5	3							
	5/25/77*	1,065	31	160	849	16	7	2							

* Several eggs had hatched by these dates so both eggs and chicks were counted to determine clutch size.

Large males and small females were sexed at a distance by the male's larger bill, head, and body size and in a few cases by their copulatory behavior. I usually made these observations using a spotting scope from a blind 25–50 m away. To check my accuracy, I captured 15 of these birds, sexed them by laparotomy, and found that all had been sexed correctly. This method did not seem adequate, however, in distinguishing between large females and small males. Consequently, I captured intermediate-sized gulls either with a walk-in funnel trap placed over the nest or by noosing incubating birds (Miller 1974). These gulls were then sexed by bill measurements (Ryder 1978) and, if doubt remained, by laparotomy. At approximately 15% of these nests, the occupants were sexed by laparotomy, 35% were sexed by measurement, and 50% by observation. The identity of most female pairs and polygynous associations was confirmed either by measurement or laparotomy. I excluded from this analysis those nests where I did not sex all incubating birds. After sexing the attendants, I monitored a nest for several days in order to confirm that all attendants had indeed been identified and sexed, and that all of the birds that I attributed to a nest were still attending it.

RESULTS

SEASONAL VARIABILITY IN SNCS

The number and frequency of SNCs slowly increased in the Ring-billed and California gull colonies until 12–14 May, when most gulls were approximately midway through the incubation period. Thereafter the number and frequency of SNCs changed little until after chicks started to hatch (Table 1).

FREQUENCY OF SNCS IN DIFFERENT COLONIES AND YEARS

In Washington and Oregon, 0.8% of the examined Ring-billed Gull nests ($n = 20,353$)

TABLE 2. Percent occurrence of supernormal clutches in different colonies combining five years of data.

	Ring-billed Gulls			California Gulls		
Colony	Number observed	4-egg clutches	5–6-egg clutches	Number observed	4-egg clutches	5–6-egg clutches
Sprague Lake	3,903	2.3	1.3	376	2.1	0.0
Banks Lake	1,821	1.6	0.8	1,045	0.8	0.0
Potholes Res.	4,494	1.9	0.2	162	0.0	0.0
Island 18	3,861	1.8	1.0	817	0.9	0.2
Island 20	4,100	1.1	0.9	852	1.2	0.1
Miller Rocks	233	1.3	0.4	1,304	1.0	0.0
Three-mile Canyon	1,761	1.2	0.7	684	0.4	0.0
Little Memaloose	0	–	–	868	1.3	0.2
Cabin Island	180	1.7	1.7	9	0.0	0.0
Total	20,353	1.7	0.8	6,117	1.0	0.1
χ^2		20.74*	36.21*		10.57	

* $P < 0.01$.

TABLE 3. Percent occurrence of supernormal clutches in different years combining data from all colonies in Table 2.

	Ring-billed Gulls			California Gulls		
Year	Number observed	4-egg clutches	5–6-egg clutches	Number observed	4-egg clutches	5–6-egg clutches
1976	109	3.7	0.9	0	—	—
1977	1,384	1.5	1.0	998	1.1	0.0
1978	2,414	2.0	1.2	1,962	1.2	0.3
1980	3,331	2.1	1.4	571	1.1	0.0
1981	13,115	1.5	0.6	2,586	0.7	0.0
Total	20,353	1.7	0.8	6,117	1.0	0.1
χ^2		9.21	27.01*		3.57	

* $P < 0.01$.

TABLE 4. Identity of breeding groups attending nests with different-sized clutches.

Breeding group	Clutch size 1	2	3	4	5	6
	Ring-billed Gulls					
♂♀	10	12	11	14	0	0
♀♀	0	0	1	5	5	4
♂♀♀	0	0	0	1	1	1
♀♀♀	0	0	0	0	1	0
	California Gulls					
♂♀	1	5	10	8	0	0
♀♀	0	1	0	3	1	0

contained five or six eggs and 1.7% contained four eggs; 0.1% of the California Gull clutches ($n = 6,117$) had five or six eggs and 1.0% had four eggs (Tables 2 and 3). Both clutches of four eggs and five to six eggs of the Ring-billed Gull varied significantly between colonies, based on data from all years, but this was not true for California Gulls. Likewise, both clutches of four eggs ($\chi^2 = 31.95$, $P < 0.01$) and five or six eggs ($\chi^2 = 23.70$, $P < 0.01$) of the Ring-billed Gull varied significantly among colonies sampled in both 1978 and 1981, but SNCs in California Gulls did not ($\chi^2 = 2.81$).

The frequency of five- or six-egg clutches in Ring-billed Gulls varied significantly among years based on data from all colonies, but not for four-egg clutches of either Ring-billed or California gulls (Table 3). At the Island 18 and Island 20 colonies, both 4-egg and 5–6-egg clutches in Ring-billed Gulls varied significantly among years ($\chi^2 = 19.80$, $P < 0.01$, and $\chi^2 = 16.90$, $P < 0.01$, respectively) as did the frequency of California Gull SNCs ($\chi^2 = 8.26$, $P < 0.05$).

The frequency of four-egg clutches correlated significantly with that of five- and six-egg clutches in Ring-billed ($r = 0.62$, $P < 0.01$) and in California gulls ($r = 0.67$, $P < 0.01$). In contrast, the frequencies of SNCs between the two species did not correlate significantly ($r = 0.17$).

NEST ATTENDANTS

In Ring-billed Gulls, I captured female-female pairs from 75% of the examined five- or six-egg clutches ($n = 12$) and 25% of the four-egg clutches ($n = 20$). A female pair was also captured from one of 34 normal-sized clutches (Table 4). Polygynous groups were found at 17% of the five- or six-egg clutches ($n = 12$). One five-egg clutch was incubated by three females (sex confirmed by laparotomy); I never found any males at this nest over three weeks.

Among California Gulls, I captured a pair of females from the only five-egg nest that was checked; of the 11 examined four-egg clutches, 27% were those of female pairs and the remaining 73% were from heterosexual pairs. One female pair attended a two-egg clutch.

DISCUSSION

SEASONAL VARIABILITY IN SNCS

The seasonal changes in SNC frequencies in my colonies indicate that the loss of SNCs owing to loss of eggs was either minimal or counterbalanced by the continual creation of new SNCs. My results contrast with those found by Ryder and Somppi (1979) at a Ring-billed Gull colony in Lake Superior. Most of the SNCs they found had been laid during the early incubation period and had become normal-sized clutches, owing to egg loss, by the end of the incubation period. The pattern of decreasing SNC frequency that they found, however, may not be typical. Lagrenade and Mousseau (1983) found no significant difference in egg loss from nests attended by female-female pairs and male-female pairs in a Ring-billed Gull colony in Montreal, Canada. In Herring Gulls, SNCs are prevalent in the late incubation period (Shugart 1980) and in Western Gulls their frequency is relatively stable throughout the incubation period (Schreiber 1970).

YEARLY AND LOCATIONAL VARIABILITY OF SNCS

The frequency of SNCs in Ring-billed Gulls in Washington varied significantly among both colonies and years. In California Gulls, the frequency of SNCs did not vary among either colonies or years when all data were pooled, but did vary among years when data from individual colonies were examined. The reason for this variability in the frequency of SNCs is uncertain but may be due to differences in certain local conditions. Such factors as food supply and egg predation may influence the proportion of MFAs that produce and retain a five- or six-egg clutch. For instance, the food supply could affect the frequency of SNCs by changing the number of MFA females that can produce a full complement of eggs. This seems plausible, especially since females who are paired together do not receive any food supplements from their nest partners, and polygynous females probably receive only half the amount that monogamous females do. The lack of correlation in SNC frequencies between the two gull species, however, suggests that they are not being equally influenced by the same local conditions.

Variations in the frequency of SNCs among colonies and years may also be attributable to fluctuating egg predation pressure because female pairs often lose eggs (Ryder and Somppi 1979). Possibly, egg predation by other gulls increases, for instance, when food is scarce or when cannibalistic gulls become more frequent in a certain colony (Pierotti 1980).

NEST ATTENDANTS OF SNCS

I found MFAs at each of the 13 nests containing five or six eggs examined in this study. The five California Gull MFAs I checked were all female pairs. In Ring-billed Gulls, 84% of the 19 examined MFAs consisted of only females and 16% had an associated male. Since many of the four-egg clutches and most of the five- or six-egg clutches in these two species were produced by female-female pairs, SNC frequencies can be used to monitor the frequency of these pairings.

Polygyny has previously been detected in Ring-billed Gulls (Conover et al. 1979, Lagrenade and Mousseau 1983). It also occurs in Herring Gulls (Shugart 1980) but in that species, polygynous females usually lay eggs in separate nests built close together. I have not seen any such double-nests of Ring-billed or California gulls in Washington colonies.

The nesting group of three female Ring-billed Gulls is, to my knowledge, the first such reported in gulls. It resembles a polygynous group of three female Ring-billed Gulls found by Conover et al. (1979a). Ring-billed Gulls can form various nesting associations within the same colony. It is unclear what maintains such diversity, especially since the reproductive success of females paired with males is significantly higher than for females paired together (Kovacs and Ryder 1983). Perhaps monogamy is the preferred breeding association of female gulls but some females are unable to obtain male mates. They may then form an alternative association rather than forego breeding entirely.

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