FEMALE–FEMALE PAIRS AND OTHER UNUSUAL REPRODUCTIVE ASSOCIATIONS IN RING-BILLED AND CALIFORNIA GULLS

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ABSTRACT.—Most Ring-billed Gulls (*Larus delawarensis*) and California Gulls (*L. californicus*) form monogamous, heterosexual pairs during the breeding season. We report here the discovery of low frequencies (1–2%) of female-female pairings in Ring-billed and California gulls in three colonies in eastern Washington. The nests of these female-female pairs usually contained 5–6 eggs rather than the more normal 2–3. Between 60–70% of the eggs in the nests of the female-female pairs were fertile. We also found evidence of brood parasitism, which appears to be one cause of 4-egg clutches, and one case of polygyny in the Ring-billed Gulls. This polygynous association built a single communal nest that was incubated by three females and one male and apparently contained the eggs of at least two females. *Received 13 November 1978, accepted 21 November 1978.*

GULLS characteristically form monogamous, heterosexual pair-bonds and lay 2- or 3-egg clutches (Paludan 1951, Tinbergen 1953). In the Western Gull (*Larus occidentalis*), however, up to 14% of the nests from colonies in the California Channel Islands contain 4–6 eggs, most of which are infertile (Hunt and Hunt 1977). These supernormal clutches (4–6 eggs) apparently are laid by two females that share incubation and chick-rearing duties. Males are seldom observed at these nests. Supernormal clutches also occur in colonies of the Ring-billed Gull (*L. delawarensis*) and the California Gull (*L. californicus*), two species differing from the Western Gull in several aspects of their breeding biology. Whereas the Western Gull is nonmigratory and spends much of the year on widely dispersed territories on the marine islands where it breeds, the Ring-billed and California gulls are migratory, stay in the nesting grounds only during the breeding season, and breed in dense colonies located on islands of inland lakes and rivers.

METHODS

On 12–13 May 1978 we surveyed three mixed-species colonies of Ring-billed and California gulls (Sprague Lake, Banks Lake and Potholes Reservoir colonies) in eastern Washington to determine the frequency of supernormal clutches, egg fertility, and female-female pairs. These colonies are described by Conover et al. (in press). Egg fertility was determined by opening eggs in the field and inspecting them for developing embryos or for lacunae in the blastodisc, which indicates infertility (Hunt and Hunt 1977). To determine the sex of birds associated with various sized clutches, adults of both species of gull were noosed on their nests (Miller 1974) at the Sprague Lake colony and sexed by laparotomy (Hunt and Hunt 1977). Sexed birds were banded, dye-marked or wing-tagged, and released. The nests occupied by these gulls were subsequently observed at repeated intervals over the next month to determine whether they were brooded and attended solely by the marked birds.

RESULTS AND DISCUSSION

We found that 3.3% of all Ring-billed Gull clutches examined contained more than 3 eggs (Table 1). Fertility in 5- and 6-egg clutches was less than that found in

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TABLE 1. The frequency and fertility of supernormal clutches from three Ring-billed Gull colonies in Washington.

Clutch size	Number of clutches examined					Egg fertility	
	Sprague Lake colony	Potholes Reservoir colony	Banks Lake colony	Total	%	Number of eggs examined	% fertile
1–3	744	512	358	1,614	96.7	20	90.0
4	17	8	9	34	2.0	52	90.4
5	11	0	5	16	1.0	41	65.9
6	3	1	1	5	0.3	23	69.9
Total	775	521	373	1,669	100.0	136	79.4

clutches of 3 or fewer eggs (Table 1), but, unlike the supernormal clutches reported in Western Gulls (Hunt and Hunt 1977), 65–70% of the eggs in 5- and 6-egg clutches showed development. Fertility of 4-egg clutches collected from Ring-billed Gulls was equivalent to that of 3-egg clutches (Table 1). This high level of fertility contrasts with the reduced fertility recorded in clutches of similar size found in Western Gull nests (Hunt and Hunt 1977).

Laparotomies of gulls that were incubating clutches of different sizes showed that the supernormal clutches of Ring-billed Gulls are related to several different types of reproductive associations (Table 2). From nests with 5 or 6 eggs we captured a preponderance of females, including 4 female-female pairs, a male-female pair, and a male and three females that were caught while incubating eggs in the same nest. This last nest is unlike any found in Western Gulls and represents the second instance of polygyny reported in larids. Shugart and Southern (1977) found that in Herring Gulls (*L. argentatus*) two females mated to the same male often built two nests spaced unusually close together. This differs from our observation, where polygynously-mated females all used the same nest to lay their eggs. The one 5-egg clutch incubated by the male-female pair was deserted within a day after the gulls' capture, so the possibility cannot be excluded that additional gulls were also associated with this nest.

Female-female pairs do not seem to account for 4-egg clutches in Ring-billed Gulls (Table 2). An equal number of males and females were captured from 4-egg clutches, including four male-female pairs. Apparently the 4-egg clutches result either from some heterosexually-mated females being able to lay four eggs or from brood parasitism in which a female lays an egg in another gull's nest. Ring-billed Gull eggs vary in spotting pattern and color, and greater variability occurs among different clutches than within the same clutch. Thus if brood parasitism occurs, 4-egg clutches should exhibit greater variability than normal 2- or 3-egg clutches. To test this hypothesis, clutches were rated on the basis of their color and spotting variability, and we found that 4-egg clutches (as well as 5- and 6-egg clutches) were indeed more varied than normal-sized clutches. Notably at the Sprague Lake Colony, where Ring-billed and California gulls nest together, a Ring-billed Gull egg was found in a nest with three California Gull eggs incubated by two California Gulls. To verify the identification, the egg was artificially incubated, and a Ring-billed Gull chick hatched from it. Hence, brood parasitism does occur, although the extent of its contribution to 4-egg clutches remains unknown.

We also captured gulls incubating 2- or 3-egg clutches to ascertain the sexual composition of pairs of gulls incubating normal clutches. The data indicate that,

TABLE 2. Sex of Ring-billed Gulls captured while incubating different-sized clutches.

Gulls captured per nest	Clutch size		
	2–3	4	5–6
1 male	4	2	0
1 female	2	2	2
1 female & 1 male	8	4	1
2 females	1	0	4
3 females & 1 male	0	0	1
Total males	12	6	2
Total females	12	6	14

while most normal-sized clutches are incubated by heterosexual pairs, some 3-egg clutches are the result of female-female pairings (Table 2). Thus, the frequency of female-female pairs may be higher than the number of 5- and 6-egg clutches.

The status of the males fertilizing many of the 5- and 6-egg clutches was not known. While one male was mated polygynously with three females at one nest, at four other nests with 5–6-egg clutches pairs of females were captured and no other gulls were subsequently seen at their nests. Yet 16 of the 22 eggs collected from these four nests were fertile. The source of fertility in these cases remains unclear. Possibly males were paired with the two females early in the reproductive period but then deserted them. Alternatively, the fertility may result from promiscuous matings. Promiscuous matings have been observed in the Western Gull (Hunt and Hunt 1977) and by the senior author in the Ring-billed Gull.

We also examined 416 California Gull nests in these three colonies and found seven (1.7%) containing four eggs. From two of these nests we captured all incubating occupants and found a male-female pair at one and a female-female pair at the other. Nine of 10 eggs examined from these 4-egg nests proved fertile, including three of the four incubated by the female-female pair.

Our results, and those of Hunt and Hunt (1977) and Ryder and Somppi (1979), show that female-female pairing is more widespread among the larids than previously realized. With documentation from four populations of three species, there is a clear need for an understanding of why and how these pairings take place. Given the widespread occurrence of female-female pairings and the finding of high levels of fertility in the eggs of female-female pairs both in this study and that of Ryder and Somppi (1979), the phenomenon cannot be dismissed as a unique event peculiar to southern California, but rather seems an occurrence of evolutionary significance.

We do not know the adaptive significance of female-female pairing. In Western Gulls on Santa Barbara Island, California, it appears that there is an excess of females (Wingfield et al. unpublished observations). If this is the case in colonies where female-female pairing occurs, then this homosexual pairing may be a strategy whereby females otherwise unable to obtain a male mate and produce offspring can still increase their chances of raising young. In this case there will be strong selection pressure for an increased frequency of promiscuous matings. Also, a female deserted by a male subsequent to mating could increase her chances of successfully fledging young if she remated with a female when no males were available. The occurrence of a polygynous association at a nest containing a supernormal clutch raises the possibility that female-female pairing may also be an alternate route to polygyny.

The high frequency of fertility in the eggs of female-female pairs [14% in the Western Gulls on Santa Barbara Island (Hunt and Hunt 1977), 31% in the Ring-

billed Gulls in the Great Lakes (Ryder and Somppi 1979), and 65–70% in the Ring-billed Gulls in Washington (this study)] shows that the incidence of promiscuous matings may be much higher in these colonial birds than formerly supposed. Given these findings and those of Bray et al. (1975), we need to consider the potential genetic impact of widespread promiscuous mating in a colony on the evolution of social behavior. If the genes of a male are likely to be carried by the chicks in neighboring territories, a male may well behave in a more tolerant manner toward these chicks than his female mate who is unrelated to them. We clearly need to increase our understanding of the genetic relationships of colony members and the impact of these relationships (Sherman 1977).

Intraspecific brood parasitism provides either paired or unpaired females the opportunity of increasing their reproductive output at the expense of other birds. This strategy probably will be successful only when the female lays her egg in a host nest at about the time the clutch in that nest is completed. Eggs laid in a nest after the clutch in the host nest is completed will have a low probability of survival, because a newly-hatched chick may not be able to compete for food against its larger nest mates, and because the parents and their chicks often leave the nest a few days after the first chicks hatch. Pairing with another female or joining a polygynous association may provide a female with the opportunity to raise some of her own offspring, although the relative success of females in these associations will probably be less than for females paired monogamously with males. A polygynous female or a female in a homosexual pair may end up caring only for another female's offspring. However, during food shortages severe enough that most monogamous pairs are incapable of finding enough food to feed one chick, nests cared for by three adults may have a competitive advantage, because two gulls can be searching for food simultaneously instead of just one.

Acknowledgments

We thank Denise Conover, Maura Naughton, Herb Senft, and Melody Roelke for their aid in the gull colonies and/or their comments on the manuscript.

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