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EXPERIMENTAL EVIDENCE THAT FEMALE-FEMALE PAIRS IN GULLS RESULT FROM A SHORTAGE OF BREEDING MALES

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ABSTRACT.—We tested the hypothesis that female-female pairings in Ring-billed (*Larus delawarensis*) and California gulls (*L. californicus*) result from a shortage of males in the breeding population. This hypothesis was tested by removing males from one Ring-billed and four California gull colonies early in the breeding season. The frequency of 4–6 egg clutches, which we used as an index of female-female pairings, was significantly higher in these colonies than in nearby control colonies, thus supporting our hypothesis. Our results indicate that female-female pairings allow females the chance to breed when they are unable to obtain a male partner.

Although terns and gulls are usually monogamous, female-female pairings have recently been discovered in Caspian Terns (*Sterna caspia*; Conover 1983), Western Gulls (*Larus occidentalis*; Hunt and Hunt 1977), Ring-billed Gulls (*L. delawarensis*; Ryder and Somppi 1979, Conover et al. 1979a), California Gulls (*L. californicus*; Conover et al. 1979a) and in the Great Lakes population of Herring Gulls (*L. argentatus*; Fitch 1980). Both females in a same-sex pair defend a single territory and lay eggs in the same nest, often resulting in a supernormal clutch of 4–6 eggs, double the normal number of 2–3. Both females incubate and share other parental responsibilities.

Much interest has centered on why one female would pair with another, because the reproductive success of these females is often much lower than that of heterosexually-paired females (Hunt and Hunt 1977). One hypothesis (Wingfield et al. 1980a, b, 1982) is that the behavior results from a pairing preference of some females for the wrong sex, perhaps owing to behavioral or endocrine masculinization of these females. Wingfield et al. (1980a, b, 1982) and Hunt et al. (1984), however, found no significant hormonal or behavioral differences between homosexually- and heterosexually-paired females in Western Gulls.

A second hypothesis proposes that female gulls pair together when they are unable to obtain male mates, owing to a shortage of breeding males (Hunt and Hunt 1977, Conover et al. 1979a, Fry and Toone 1981, Pierotti 1981). This hypothesis was supported by the observation that females outnumbered males three-to-two in a Western Gull colony where female-female pairings occur (Hunt et al. 1980). We tested this hypothesis by experimentally manipulating the sex ratio of breeding adults at some small colonies of Ring-billed and California gulls. By doing so, we hoped to answer the question of why two females would pair together rather than with male mates. Previous authors have suggested that mating systems are either unrelated to sex ratios (Verner 1964; Wittenberger 1976, 1979) or influence sex ratios (Hamilton 1967, Wilson and Colwell 1981). In the case of these gulls, we were testing the hypothesis that sex ratios determine the mating system used.

METHODS

If a shortage of males in a breeding population leads to female-female pairings, then removing males from the colony should lead to an increase in the frequency of such pairings in colonies where female-female pairs already occur. In 1981 we removed males from one Ring-billed Gull colony and four California Gull colonies; we compared the frequency of female-female pairings in these colonies to those in nearby (control) colonies where no males were removed. All colonies were located in Washington and Oregon and are described elsewhere (Conover et al. 1979b).

We captured gulls from the experimental colonies by first baiting them on islands located within 100–200 m of the colony and in nearby garbage dumps, and then firing a rocket net over them. All trapping was done early in the 1981 breeding season (March and April), when gulls were starting territorial defense and courtship but before they began copulating.

We captured gulls at six sites close to the four experimental colonies but not inside them. Prior experience had taught us that if in-colony capture were attempted before the incubation period, many of the gulls would desert the colony. Birds from the Potholes Reservoir colony

TABLE 1. Frequency of supernormal clutches in experimental and control California Gull colonies in 1981 and in previous years.

	1981				Previous years (1976–1980)		
	% males removed	# nests	% supernormal clutches		# nests observed	% supernormal clutches	
			4 eggs	5–6 eggs		4 eggs	5–6 eggs
Experimental colonies							
Cabin Island	35.3	11	9.1	0.0	9	0.0	0.0
Little Memaloose	18.2	243	2.1	0.8	868	1.3	0.2
Miller Rocks	4.0	312	0.3	0.3	1,304	1.0	0.0
Potholes	4.3	1,369	1.9	0.1	162	0.0	0.0
Total	7.6	1,935	1.7	0.3	2,343	1.0	0.1
Control colonies							
Banks	0	838	0.7	0.0	207	1.0	0.0
Island 20	0	511	1.2	0.0	341	0.9	0.3
Island 18	0	411	0.5	0.0	406	1.2	0.4
Three-mile Canyon	0	684	0.4	0.0	0	—	—
Sprague	0	142	0.7	0.0	234	3.0	0.0
Total	0	2,586	0.7*	0.0	1,188	1.5	0.3

* $P < 0.01$ (experimental vs. control colonies).

were trapped on sand dune islands 100 m north of the colony and at a garbage dump 8 km distant. The nearest control colony (Banks Lake) was 60 km away. Gulls from the Cabin Island colony were netted on a pebble beach 100 m distant and on a lawn on the edge of the lake across from the colony (1 km away). Island 18 colony, the nearest control colony, was 67 km distant. Birds from the Miller Rocks colony were trapped at a dump 0.8 km distant and those from the Little Memaloose colony were trapped on the lakeshore 1 km distant. The control colony (Three-mile Canyon) closest to these two trapping sites was 80 km distant.

Both Ring-billed Gulls (Ryder 1978) and California Gulls (Conover, unpubl. data) were initially sexed by bill and head measurements (males being slightly larger). Birds of intermediate size, which could not be reliably sexed by measurement, were either laparotomized or released. Most captured females were immediately banded with colored leg bands and U.S. Fish & Wildlife Service aluminum bands and were released; males from experimental colonies were kept in captivity until after the egg-laying period and then were released unharmed. We did some trapping at control colonies but all birds (including males) there were immediately color-banded, sexed, and released.

To determine whether the trapped gulls did, in fact, come from the nearby experimental colonies, we searched for the banded gulls in both experimental and control colonies. We repeatedly observed the color-banded birds in the colony nearest the trap site; we never found any in another colony. While this does not preclude the possibility that some of the males trapped near experimental colonies may have come from control colonies, it seems safe to assume that most came from the experimental colonies.

Altogether, we removed 135 male California Gulls from four colonies and 77 male Ring-billed Gulls from one colony. We estimated that we removed a maximum of 4 to 35% of the male California Gulls from the four colonies and 23% of the male Ring-billed Gulls from the single colony manipulated (Tables 1 and 2). We assumed that the number of breeding males at each colony during the start of the 1981 breeding season equalled the number of nests in that colony during 1981 plus the number of males we had removed. These figures should be considered maximum estimates because they are based on the assumption that all removed males came from the experimental colonies.

We estimated the frequency of female-female pairings in each colony by counting the supernormal clutches (4–6 eggs) about 15 May, which was the middle of the incubation period and the time when supernormal clutches were most numerous in these colonies (Conover 1984). In past years (1976–1980), clutches were counted from 12–22 May with all but a few colonies surveyed from 13–18 May. To determine whether manipulating the sex ratio of the population increased female-female pairings, we compared the frequency of supernormal clutches in the experimental colonies to their frequency in nearby control colonies during the same year. The data from control and experimental colonies were compared using contingency tables corrected for continuity. In previous years, the frequency of supernormal clutches was not significantly different between the colonies that we used as treatments and controls in 1981.

TABLE 2. Frequency of supernormal clutches in experimental and control Ring-billed Gull colonies in 1981 and previous years.

	1981				Previous years (1976–1980)		
	% males removed	# nests	% supernormal clutches		# nests observed	% supernormal clutches	
			4 eggs	5–6 eggs		4 eggs	5–6 eggs
			Experimental colony				
Cabin Island	22.5	265	4.2	2.3	180	1.7	1.7
			Control colonies				
Banks	0	1,448	1.4	0.6	373	2.4	1.6
Island 20	0	2,495	0.8	0.8	1,605	1.6	0.8
Island 18	0	2,558	1.2	0.6	1,303	2.8	1.6
Miller Rocks	0	96	2.1	1.0	137	0.7	0.0
Potholes	0	3,773	2.0	0.2	721	1.7	0.1
Three-mile Canyon	0	1,761	1.2	0.7	—	—	—
Sprague	0	975	3.4	0.7	2,928	1.9	1.4
Total		13,106	1.5*	0.6*	7,067	2.0	1.2

* $P < 0.01$ (experimental vs. control colonies).

We were unable to determine directly the frequency of female-female pairings in these colonies. This would have required trapping a large number of gulls from each of these colonies for sexual identification, a logistical impossibility. Furthermore, such an operation would have biased the results because trapping so many gulls inside a colony would have caused a high proportion of nesting gulls to desert the colony. Instead, we used the frequency of supernormal clutches as an index of female-female pairs. Many investigators have shown that most 5–6-egg clutches in Ring-billed Gulls (Conover et al. 1979a, Ryder and Somppi 1979, Lagrenade and Mousseau 1983, Conover 1984) and California Gulls (Conover et al. 1979a, Conover 1984) result from female-female pairings. Female-female pairings are also responsible for approximately 30% of the 4-egg clutches in Ring-billed and California gulls in Washington state (Conover 1984). Consequently, an increase in the frequency of female-female pairings should increase the number of 4-egg clutches as well as 5- to 6-egg clutches. Frequencies of both 4-egg and 5- to 6-egg clutches should be valid indices of female-female pairing frequencies, assuming that the proportion of supernormal clutches attended by female-female pairs is similar in both experimental and control colonies. We believe this to be the case.

RESULTS

Four-egg clutches were significantly more frequent in the California Gull colonies where males had been removed than in control colonies (Table 1). Additionally, we found four 5- to 6-egg clutches in the experimental colonies while none were found in the control colonies. The differences between these experimental and control colonies reflected both an increase in supernormal clutches in experimental colonies and a decrease in supernormal clutches in control colonies during 1981—changes in their frequencies from past years. In each experimental colony except Miller Rocks, the frequency of 4- to 6-egg clutches in 1981 exceeded the highest frequency found in the same colony in past years (1977, 1978, and 1980) based on a total of seven prior reports.

We obtained similar results for the Ring-billed Gulls (Table 2). In the experimental colony, both 4- and 5- to 6-egg clutches were significantly more frequent than in control colonies. These differences were due both to an increase over previous years' levels in the frequency of supernormal clutches in experimental colonies and a decrease from previous levels in their frequency at control colonies. Both 4-egg and 5- to 6-egg clutches were more frequent in the experimental colony than in any of the control colonies in 1981 and were also higher than observed in any of the 15 reports of clutch-size frequencies made in any of these gull colonies during the five previous years.

DISCUSSION

Our study tested the male shortage hypothesis for the formation of female-female pairs by removing adult males early in the breeding season from several Ring-billed and California gull colonies. We found that 4- to 6-egg clutches were more frequent in these colonies than in control colonies from which no males were removed. We believe that the increase in supernormal clutches was due to an increase in the number of female-female pairs, in turn the result of the decreased availability of males in the breeding population. Adult females were also in excess in the only gull colony with female-female pairings for which the adult sex ratio was investigated (Hunt et al. 1980).

Our findings indicate that the sex ratio of breeding adults may determine the mating system used by these gulls, and that female-female pairings may be an adaptive response of females who are unable to obtain male mates. Some female-female pairs fledge young, their eggs being fertilized through promiscuous matings with males (Hunt and Hunt 1977, Conover et al. 1979a). Hence, the formation of female-female pairings enhances the ability of females to raise young when they are unable to find male mates. This is especially true considering that individual gulls cannot successfully raise young by themselves; the eggs and chicks require constant protection from neighboring gulls, which leaves no time for foraging.

Our results do not mean that female-female pairings will always result when females outnumber males. The formation of a female-female pair is only one of several options open to unmated females. Others include: 1) not breeding at all and trying again next year; 2) becoming a nest helper to a male who has lost his mate in order to increase the prospects of pairing with the same male next year (Western Gulls: Pierotti 1980); 3) dump nesting (Ring-billed Gulls: Ryder and Somppi 1979); 4) trying to join a heterosexual pair to form a polygamous group (Ring-billed Gulls: Conover et al. 1979a, Lagrenade and Mousseau 1983; Herring Gulls: Fitch 1980). Additionally, female-female pairs may not occur in populations or colonies where space for breeding territories is limited because they cannot compete with the larger males for territories. This is apparently the case on the Farallon Islands, where Pierotti (1981) found that some females were unable to obtain male mates but none of them formed female-female pairings.

Our results also do not mean that the presence of a few female-female pairings in a population signifies that the sex ratio of that population must be skewed. Even if males and females are present in equal numbers, some females may be unable to find unpaired males. Additionally, the presence of female-female pairs may indicate potential difficulties in recognizing the sex of a potential partner (Hunt 1980, Burley 1981, Hunt et al. 1984). Nevertheless, a substantial change in the frequency of supernormal clutches or female-female pairs in a population may indicate that a change has occurred in the sex ratio of breeding adults. Thus, the frequency of supernormal clutches may prove a useful indicator for monitoring major changes in adult sex ratios.

Our experiment leaves unanswered the question of why the sex ratio among breeding adult gulls should be skewed. One possibility is higher male mortality; Coulson and Wooler (1976) showed that more male than female Kittiwakes (*Rissa tridactyla*) die during the breeding season. Another potential cause of a skewed sex ratio is DDT feminization of male gull embryos (Fry and Toone 1981). Although feminization does not cause a complete sex reversal, it may prevent males from breeding, effectively skewing the breeding adult sex ratio. Our findings indicate that an excess of breeding females, for whatever reason, would likely result in the occurrence of female-female pairings.

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RECENT PUBLICATIONS

Distribution of Oklahoma birds.—D. Scott Wood and Gary D. Schnell. 1984. University of Oklahoma Press, Norman. 209 p. Paper cover. $14.95. Maps and bar graphs summarize volumes of information in this useful state book. Three hundred and eighty species, arranged by family and subfamily, are depicted on an outline map of Oklahoma counties, in which sight records and specimens are indicated by symbols. Letters are added to indicate season and status. A simple bar graph designates relative seasonal abundance. The only text occurs in the preface, where the symbols used later are explained. Three summary figures provide specimen data and species known in each county. Appendix of accidentals and other species. Index. Drawings of Sprague's Pipit on cover and frontispiece by Robert M. Mengel. Comprehensive (more than 14,000 sightings and specimens examined) and concise (maps and graphs only), this is an essential reference on the occurrence and status of birds in Oklahoma.—J. Tate.

Oklahoma ornithology/an annotated bibliography.—Joseph A. Grzybowski and Gary D. Schnell. 1984. The University of Oklahoma Press, Norman. 192 p. $19.95. "We have prepared this annotated bibliography of Oklahoma ornithology as an easy reference for persons interested in conducting research and surveys on Oklahoma birds, and for others needing access to information on the state's avifauna." Over 1,500 references have been sifted from periodicals of ornithology, wildlife management, and ecology, as well as dissertations, Pittman-Robertson reports, environmental assessment reports, and various other publications. Indices according to key words, bird families, and common names give access to the bibliography. Three appendices list citations of Christmas Bird Counts, seasonal reports, and surveys of breeding birds in Oklahoma, as given in *Bird-Lore, Audubon Magazine,* and their successors.