

FEMALE-FEMALE PAIRING AND SEX RATIOS IN GULLS: AN HISTORICAL PERSPECTIVE

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The regular occurrence of supernormal clutches (SNCs) in several North American gulls has led to the discovery of female-female pairings in the Western Gull (*Larus occidentalis*) (Hunt and Hunt 1977), Ring-billed Gull (*L. delawarensis*) (Ryder and Somppi 1979, Conover et al. 1979), Herring Gull (*L. argentatus*) (Fitch 1980, Shugart 1981), and Caspian Tern (*Sterna caspia*) (Conover 1983). While some SNCs may result from polygynous associations (Conover et al. 1979, Lagrenade and Mousseau 1983, Conover 1984a), nest parasitism (Fetterolf and Blokpoel, in press) and egg dumping (Ryder and Somppi 1979), most SNCs have resulted from female-female pairs (Hunt and Hunt 1977, Ryder and Somppi 1979, Conover et al. 1979, Conover 1983, Lagrenade and Mousseau 1983, Conover 1984a). Hence, SNC frequencies are often used as an index of female-female pairing frequencies.

It is unclear why some females pair together rather than with male mates because the reproductive success of these females is often lower than for females paired with males (Hunt and Hunt 1977, Kovacs and Ryder 1983). One hypothesis is that some females pair with the wrong sex due to female masculinization, but this hypothesis has not been supported by the finding that there are no significant hormonal (Wingfield et al. 1982) or behavioral (Hunt et al. 1984) differences between females paired with other females and those paired with males in Western Gulls.

Another hypothesis proposes that female-female pairings occur when some females are unable to obtain male mates (Hunt and Hunt 1977). This hypothesis has been supported by two recent studies. Hunt et al. (1980) found that female Western Gulls outnumbered males in a colony on Santa Barbara Island where female-female pairs are common. Furthermore, Conover and Hunt (1984) tested this hypothesis by experimentally skewing the breeding adult sex ratio at some small Ring-billed and California (*L. californicus*) gull colonies by removing males. They found that SNC frequencies in these colonies were significantly higher than in nearby control colonies.

In this study, we have further evaluated this hypothesis by testing the prediction that females should outnumber males in those gull species and populations where female pairings occur: Ring-billed, California, Herring, and Western gulls. There are historical differences in the occurrence of female-female pairing in these four gull species. In Ring-billed and Cal-

ifornia gulls, SNCs are regularly found in some of the earliest egg collections and literature reports (Conover, 1984b). In Western and Herring gulls, however, SNCs have only been found regularly since 1950 (Hunt and Hunt 1977, Conover 1984b). Consequently, female-female pairings appear to be a new phenomenon in the latter two species but not in the Ring-billed and California gulls. If the male shortage hypothesis is correct, these differences should correspond with sex ratio differences. In this study, we examined the thousands of gull specimens in museum collections to test the following predictions: (1) in Ring-billed and California gulls, adult females should outnumber males regardless of collection date; and (2) in the Herring and Western gulls, females should outnumber males among specimens collected since 1950 but not among those collected before 1940.

METHODS

To assess the sex ratio of gulls, we examined specimens in the U.S. and Canadian museums listed in the acknowledgments. All label data were either personally obtained by us, or in the case of collections which we were unable to visit, by the staff of the institutions in question. For each specimen, we determined its age by plumage (Dwight 1925) and obtained sex of the specimen, collection site, and date from the specimen tag. For each species, we tested whether one sex significantly ($P \leq 0.05\%$) outnumbered the other by using Chi-square tests. Chi-square contingency tables corrected for continuity were used to determine whether the sex ratio differed between specimens collected before 1940 and after 1950.

One problem with attempts to determine the sex ratio of natural populations is the uncertainty that the subjects were collected randomly, thereby reflecting the sex ratio of the population. In most studies on avian sex ratios, the investigators themselves collected the subjects from a population. The drawback of this approach is that one sex may be more vulnerable than the other to the particular collecting technique employed by the investigators or one sex may spend more time at the collection sites than the other, at least during certain hours.

In this study, we took another approach: the examination of museum collections. The advantages of this approach include the very large samples available and the fact that these specimens were collected by hundreds of people at hundreds of locations. Potential problems nonetheless exist with using museum specimens to determine the sex ratio of a population. First, most collectors probably were not concerned with collecting specimens randomly with respect to sex. For gulls, this should not be a serious problem given the similarity in appearance of both sexes; few collectors probably knew or cared which sex they were collecting. Second, one sex may be more likely collected than the other, owing to behavioral differences. Most museum specimens were shot. Burger (1983) showed that this collecting technique favored males over females in Laughing Gulls (*L. atricilla*) and this may also be true for other gull species (P. M. Fetterolf, pers. comm.). If this is true for the species used in this study, our tests for excess females will be conservative. To further evaluate this potential, we also examined museum specimens of most North American gull species (*L. atricilla*, Franklin's Gull, [*L. pipixcan*], Common Black-headed Gull [*L. ridibundus*], Bonaparte's Gull [*L. philadelphia*], Heermann's Gull [*L. heermanni*], Mew Gull [*L. canus*], *L. delawarensis*, *L. californicus*, *L. argentatus*, Thayer's Gull [*L. thayeri*], Yellow-footed Gull [*L. livens*], *L. occidentalis*, Glaucous-winged Gull [*L. glaucescens*], Glaucous Gull [*L. hy-*

TABLE 1
SEX RATIOS OF GULL SPECIMENS

Species	All specimens		Adults	
	♂/♀	N	♂/♀	N
California Gull	0.90**	1651	0.97	502
Ring-billed Gull	0.77**	2053	0.81*	569
All North American gulls	0.94	17,083	1.07**	6137

* $P \leq 0.05$ (different from 1 to 1 ratio).

** $P \leq 0.01$ (different from 1 to 1 ratio).

perboreus], Great Black-backed Gull [*L. marinus*], and Black-legged Kittiwake [*Rissa tridactyla*]) to determine the sex ratio for museum gull specimens in general.

RESULTS

In both Ring-billed and California gulls, specimens of females significantly outnumbered those of males when all age classes of each sex were pooled. In both species, adult females outnumbered males, but only in Ring-billed Gulls were there significantly more adult females than adult males (Table 1). Thus, the Ring-billed Gull data support the male shortage hypothesis, but the California Gull data do not. In contrast, males significantly outnumbered females among adult specimens when data from all North American gull species were combined. This finding reduces the likelihood that female Ring-billed and California gulls were preferentially collected or were more vulnerable than males to the employed collecting techniques.

When all age classes were combined, Ring-billed and California gull specimens had similar sex ratios before 1940 and after 1950 (Table 2). This result was predicted because there has been no change in SNC frequencies in these two species since 1950 (Conover 1984b). Too few adult Ring-billed and California gull specimens have been collected since 1950 to allow a comparison with the sex ratios of adults collected before 1940.

Among Western Gulls, the male/female ratio was lower among post-1950 than pre-1940 specimens. This difference was statistically significant for both adults alone and for all age classes combined (Table 2). In Herring Gulls, the male/female ratio for both adults and all age classes combined was also lower among specimens collected since 1950, but the differences were not statistically significant due to the small number of specimens collected since that date. These results support the prediction of a post-1940 shift in sex ratios in Western Gulls but not in Herring Gulls. Among

TABLE 2
SEX RATIOS OF GULLS COLLECTED BEFORE 1940 OR AFTER 1950

Species	All specimens				Adults			
	pre-1940		post-1950		pre-1940		post-1950	
	δ/\varnothing	N	δ/\varnothing	N	δ/\varnothing	N	δ/\varnothing	N
California Gull	0.90	1551	0.96	100	—	—	—	—
Ring-billed Gull	0.76	1971	1.05	82	—	—	—	—
Western Gull	1.04	1365	0.55**	186	1.16	471	0.43**	66
Herring Gull	0.88	2186	0.68	114	1.03	780	0.42	27
All North American gulls	0.96	14,428	0.75**	988	1.08	4273	0.82**	266

** $P \leq 0.01$, pre-1940 vs post-1950.

all North American gull species combined, the adult male/female ratio has dropped significantly from 1.08 for pre-1940 specimens to 0.82 for post-1950 specimens.

DISCUSSION

In our examination of museum specimens of gulls, we found significant intraspecific shifts in sex ratios between birds collected before 1940 and after 1950 for all North American gull species combined and for Western Gulls. Before 1940, male Western Gulls appear to have outnumbered females, but among specimens collected since 1950 females outnumber males by over 2 to 1. This significant decrease in the male/female ratio occurred at or before the recent appearance of SNCs and female-female pairs in this species.

A recent change in sex ratio may not be unique to Western Gulls. In Herring Gulls, the adult male/female ratio has dropped from 1.0 for specimens collected before 1940 to 0.5 for birds collected since 1950, although the difference is not statistically significant due to the small number of Herring Gulls collected since then. Female-female pairings may also be a recent phenomenon in this species (Conover 1984b). In contrast, there is, if anything, a slight increase in the male/female ratios of Ring-billed and California gulls from pre-1940 to post-1950, as predicted for species with a long history of SNCs.

While these estimates of sex ratio probably do not represent precisely the sex ratio in the various gull populations, the changes or lack of changes within species over time should be valid indices of the change or lack of change in the sex ratios of the populations sampled. Distortions of sex ratios due to species-specific behavior or collecting techniques are likely and are of major concern when investigators attempt to determine ab-

solute values for sex ratios or to compare sex ratios between distantly related taxa. In the present case, our comparisons are within a species over time, or between closely related species. For these very limited comparisons, there is little likelihood that the potential bias would strongly affect our results. It is unreasonable to assume that changes in either species-specific behavior or collecting techniques would cause increases in the male/female ratio for some species and decreases in others.

This study leaves unanswered the question of whether sex ratios of museum specimens accurately reflect the absolute sex ratio of gull populations. The sex ratios obtained in this study, however, are similar to those obtained by other means. Johnston (1956) found an adult male/female ratio of 0.83 for California Gulls in California. Behle (1958) sexed California Gulls at a Utah colony and found a 1.06 male/female ratio. Our study revealed a ratio of 0.97 for adult California Gull specimens, a value which falls between these two values and is not statistically different from either of them. Hunt et al. (1980) captured 606 adult Western Gulls on Santa Barbara Island in 1977 and 1978 and found a 0.26 male/female ratio. However, based on the proportion of female-female pairs in the colony, they calculated a sex ratio of 0.67. In our study, we found for post-1950 Western Gull specimens an adult sex ratio of 0.43, a value intermediate between their two reported estimates. These authors further reported that for 2–3 year old Western Gulls, the male/female ratio was 0.67, close to our value of 0.60 for immature Western Gull specimens obtained since 1950. Hence, both our results and those of Hunt et al. (1980) have shown that females significantly outnumber males in Western Gulls.

Why should there be a shortage of breeding males in some gulls? Fry and Toone (1981) hypothesized that a shortage of breeding males in Western Gulls was caused by DDT pollution. They argue that sublethal doses of DDT feminize male embryos, causing mature males to forego breeding. This would alter the adult sex ratio at breeding colonies, but not the adult sex ratio of the population as a whole. Our results suggest an alternate hypothesis. Hunt et al. (1980) found a 0.67 male/female ratio among breeding adults at one colony. This is higher than the 0.43 male/female ratio we found for adults collected since 1950. Few of the specimens in the museum collections were obtained from breeding colonies, so our value should reflect the general adult sex ratio. Thus, our data suggest that the shortage of males at the breeding colonies results from a low male/female ratio in the adult population as a whole and not from the failure of feminized males to breed. Therefore, we suggest that the recent occurrence of female-female pairings and the skewed sex ratio in Western Gulls stems from high differential male mortality.

SUMMARY

We evaluated the hypothesis that female-female pairings result from a shortage of breeding males by using museum specimens to test the hypothesis' following predictions: (1) females should outnumber males regardless of collection date in Ring-billed and California gulls, two species where supernormal clutches and presumably female-female pairings have occurred for many years; and (2) in Herring (*Larus argentatus*) and Western (*L. occidentalis*) gulls, the male/female ratio should have decreased since 1950, given the occurrence of female pairings only since then in these two species. The results showed that some, but not all, of these predictions were accurate. Based on museum collections, adult females significantly outnumbered males in Ring-billed Gulls (*L. delawarensis*) but not in California Gulls (*L. californicus*). In both Western and Herring gulls, the male/female ratio was lower among adults collected since 1950 than among those collected earlier, but the differences were not statistically significant in the latter species due to the small number of Herring Gulls collected since 1950.

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