Sex Ratios of North American Gulls Based on Museum Collections

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Abstract.—A survey of museum specimens revealed large interspecific variability in the sex ratio in 14 species of North American gulls. In the three black-headed species, (Larus atricilla, L. pipixcan, and L. philadelphia), females outnumbered males among prefledglings, but males outnumbered females among adults. In the white-headed gulls, the male/female ratio in prefledglings did not vary significantly from 1.0 in any species. However, among first-year birds, females outnumbered males in 8 white-headed species. Among adults, the male/female ratio was < 1.0 in the Mew and Ring-billed gulls, > 1.0 in the Great Black-backed Gull, and ≥ 1.0 in the other white-headed gulls.

Key words.—Gulls, kittiwake, larids, Larus, Rissa, sex ratios, sexual mortality.

Unusual intraspecific variability in mating systems has recently been observed in some North American gulls. Although these species are predominantly monogamous, polygyny has recently been observed in Herring Gulls (Larus argentatus) (Shugart and Southern 1977, Fitch 1980, Shugart 1981) and Ring-billed Gulls (L. delawarensis) (Conover et al. 1979, Conover 1984). Female-female pairings have also been discovered in Herring Gulls (Fitch 1980, Shugart 1981); Ring-billed Gulls (Ryder and Somppi 1979, Conover et al. 1979, Conover 1984); California Gulls (L. californicus) (Conover et al. 1979, Conover 1984) and Western Gulls (L. occidentalis) (Hunt and Hunt 1977).

The reasons for such diversity of mating systems within some species are unclear. Polygyny is generally believed to occur when members of a population cross the “polygyny threshold,” after which it becomes more advantageous for a female to mate with a polygamous male than to become the sole mate of a monogamous male (Verner and Willson 1966, Orians 1969). Uneven sex ratios have also been proposed as one cause of polygyny (Verner 1964, Altman et al. 1977). For most polygynous species which have been examined, however, the prefledging sex ratio was not significantly skewed (Orians 1969).

A shortage of breeding males may be responsible for female-female pairings (Hunt and Hunt 1977, Hunt et al. 1980, Conover and Hunt 1984a, 1984b). Nevertheless, a shortage of breeding males may not be sufficient for the occurrence of female-female pairs. Burger and Gochfeld (1981) presented some data indicating that female Herring Gulls may outnumber males in breeding colonies in Maine and New York, two areas where female-female pairings have not been detected.

An evaluation of these hypotheses or other theories concerning avian sex ratios is hampered by a paucity of data on the sex ratios in gull populations and other avian groups. A major difficulty with any attempt to evaluate the sex ratio of a population is the uncertainty that the sex ratio of the sampled individuals is the same as that of the population. The concern is that the sampling method may be biased and favor one sex over the other (Burger 1983). For this reason, it is worthwhile to obtain sex ratio data by as many methods as possible. In this study, we examined the sex ratios of museum specimens of North American gulls. We also tested whether intraspecific sex ratios varied among age classes, collection locations, and collection seasons.

METHODS

We examined specimens in several U.S. and Canadian museums (see Acknowledgments). For each specimen, we determined its age from its plumage (Dwight 1925) and its sex from the specimen tag. We also recorded where and when the specimen was collected. Additional data were furnished to us by the staffs of museums which we could not visit. In all, we obtained data for over 11,000 specimens.

For each species, we conducted chi-square tests to determine whether one sex outnumbered the other.
for each age class. Contingency tables corrected for continuity were used to determine whether the sex ratio changed between sequential age classes.

We also examined the data by the date of collection and location to determine if the ratio of males to females for any species differed between the breeding season (April-August) and non-breeding season, or among geographic areas. Variation among areas would be expected, for instance, if the sexes winter in different locations. Initially, we combined all age classes for this analysis. We later divided the specimens in adults and juveniles and reanalyzed the data for each group. However, for many specimens used in this part of the study, we did not have information on their age and so these specimens were deleted for this analysis. This considerably reduced sample sizes for some species.

RESULTS

Interspecific Variability

The sex ratios of the black-headed gulls (Larus atricilla, L. pipixcan, L. philadelphica) were substantially different from the other gulls (Table 1). In all three species, prefledgling females significantly outnumbered males. Among first-year and subadult specimens, however, females and males were in equal frequency in all three species. Among adults, however, males outnumbered females, the opposite of the prefledgling sex ratio.

Among the white-headed gulls, sex ratios did not differ from unity among prefledglings. For most species, however, the sex ratios changed significantly between prefledglings and first-year birds (Table 1), with first-year females outnumbering males in 7 species. Among subadult gulls, females also outnumbered males in the Heermann’s (L. heermanni), Mew (Larus canus) and Ring-billed gulls. The male/female ratio among adults was < 1.0 in the Mew and Ring-billed gull, > 1.0 in the Great Black-backed Gull (L. marinus), and = 1.0 in the other white-headed gulls.

Seasonal and Locational Variability

The sex ratio of Mew Gulls, Ring-billed Gulls, Thayer’s Gulls (L. thayeri), and Black-legged Kittiwakes (Rissa tridactyla) differed significantly between those collected during the breeding and non-breeding seasons when all age classes were combined (Table 2). When just adult specimens were examined, there were no significant differences between the breeding and nonbreeding season due in large part to the much smaller sample sizes. Among juvenile specimens, the sex ratio differed significantly between the two seasons only in one species: the Glaucous Gull.

The sex ratio of gulls collected from different sites differed significantly in the Laughing (L. atricilla), Mew, Ring-billed, Thayer’s and Glaucous-winged gulls (L. glaucescens) when all age classes were combined (Table 3). Female Laughing Gulls outnumbered males two-to-one among Central American specimens, but males predominated in all other areas. In the Ring-billed Gull, sex ratio differed between specimens collected in the eastern and the western halves of North America, with males being less common in the West. In the Mew, Thayer’s, and Glaucous-winged gulls, females outnumbered males in the more southern collecting sites but not in northern ones.

Among just adult specimens, sex ratios differed significantly among locations only in the Laughing Gull. There were no significant differences among locations for any species when just juveniles were examined.

DISCUSSION

Problems Determining Sex Ratios

Virtually all methods for assessing the sex ratio of free-ranging avian populations are subject to sampling biases. These biases include the possibility that one sex is more vulnerable to the collecting technique than the other (Burger 1983), or that behavioral differences between the sexes may make one sex more likely to be at the collection site than the other. Obviously, the more varied the localities and techniques used to obtain the sample, the less likely that any one source of bias will cause misleading results. To the extent that museum collections are made by a variety of individuals using different methods in different locations, museum-based estimates of sex ratio may be less biased than other methods but potential biases still exist with museum collections (Conover and Hunt 1984a). These problems were best illustrated by Jehl (1987). When he examined museum specimens of L. californicus collected during the breeding season, he found a 1.6 male/female ratio. However, Jehl also found a 0.6 male/female ratio in
Table 1. Sex Ratios of Different Age Classes of Museum Specimens of Gulls.

| Gull Species          | Adult Ratio | Subadult | 1st Year | Prefledglings | N         |
|-----------------------|-------------|----------|----------|---------------|-----------|
|                       | Adults      | Subadult | 1st Year | Prefledglings |           |
| Laughing              | 1.37\(^e\)  | 1.24     | 1.21\(^p\) | 0.62\(^p\)   | 672       |
| Franklin's            | 1.52\(^e\)  | —        | 1.06     | 0.63\(^p\)   | 497       |
| Bonaparte's           | 1.55\(^e,4\)| —        | 0.91     | 0.48\(^p\)   | 785       |
| Heermann's            | 0.84        | 0.48\(^e\)| 0.63     | 1.29          | 145       |
| Mew                   | 0.55\(^e\)  | 0.41\(^e\)| —        | —             | 115       |
| Ring-billed           | 0.81\(^1\)  | 0.77\(^1\)| 0.67\(^2,3\)| 1.35          | 569       |
| California            | 0.97        | 0.93\(^3\)| 0.60\(^2,3\)| 1.59          | 502       |
| Herring               | 0.99        | 1.00\(^3\)| 0.71\(^2,3\)| 1.18          | 807       |
| Thayer's              | 1.03        | 0.63     | 0.32\(^e\)| —             | 73        |
| Western Gull          | 1.13        | 1.03     | 0.77     | 1.23          | 589       |
| Glaucous-winged       | 0.88        | 0.98     | 0.72\(^e\)| 0.95          | 157       |
| Glaucous              | 0.98        | 0.73     | 0.69\(^3\)| 1.79          | 583       |
| Great Black-backed    | 1.37\(^1\)  | 1.25     | —        | 1.00          | 173       |
| Black-legged Kittiwake| 0.82        | —        | 0.86     | 0.98          | 365       |
| TOTAL                 | 1.07\(^3,4\)| 0.87\(^e\)| 0.80\(^2,4\)| 1.01          | 6092      |

\(^{1,2}\)Results of chi-square tests to test whether sex ratio of a particular age class differed significantly from unity (\(^{1}P<0.05, \(^{2}P<0.01\)).

\(^{3,4}\)Results of contingency tables corrected for continuity to test whether the sex ratio changed significantly between on age class and the next younger age class (\(^{3}P<0.05, \(^{4}P<0.01\)).
Table 2. Sex ratio of gulls collected during the breeding season and nonbreeding season.

| Gull species      | Age class | Breeding season (April-August) | Nonbreeding season (Sept.-March) | χ² |
|------------------|-----------|-------------------------------|---------------------------------|----|
|                  |           | Male/Female ratio N           | Male/Female ratio N             |    |
| Laughing         | All classes | 1.19 182                     | 0.85 102                        | 1.49 |
|                  | Adults     | 1.15 56                       | 1.25 18                          | 0.01 |
|                  | Juveniles  | 1.22 20                       | 1.33 14                         | 0.05 |
| Franklin's       | All classes | 1.08 425                      | 1.06 370                        | 0.01 |
|                  | Adults     | 1.02 89                       | 2.00 21                         | 1.18 |
|                  | Juveniles  | 1.00 20                       | 0.68 47                         | 0.20 |
| Bonaparte's      | All classes | 1.05 115                      | 1.29 87                         | 0.31 |
|                  | Adults     | 1.11 135                      | 0.76 139                        | 2.08 |
|                  | Juveniles  | 0.72 115                      | 0.81 96                         | 0.09 |
| Heermann's       | All classes | 0.63 212                      | 0.58 282                        | 0.16 |
|                  | Adults     | 0.93 58                       | 0.49 128                        | 3.43 |
|                  | Juveniles  | 0.68 62                       | 0.57 107                        | 0.11 |
| Mew              | All classes | 1.23 98                       | 0.39 392                        | 25.09|
|                  | Adults     | 1.00 12                       | 0.50 27                         | 0.39 |
|                  | Juveniles  | 1.00 10                       | 0.61 29                         | 0.08 |
| Ring-billed      | All classes | 0.91 166                      | 0.54 412                        | 7.14 |
|                  | Adults     | 1.20 33                       | 1.04 47                         | 0.00 |
|                  | Juveniles  | 0.69 61                       | 0.47 143                        | 1.10 |
| California       | All classes | 0.92 194                      | 0.65 412                        | 3.67 |
|                  | Adults     | 0.93 52                       | 0.59 100                        | 1.30 |
|                  | Juveniles  | 0.63 80                       | 0.72 188                        | 0.13 |
| Herring          | All classes | 0.72 141                      | 0.72 328                        | 0.00 |
|                  | Adults     | 0.69 22                       | 0.74 54                         | 0.01 |
|                  | Juveniles  | 0.57 11                       | 0.92 73                         | 0.16 |
| Thayer's         | All classes | 0.76 60                       | 0.32 100                        | 5.65 |
|                  | Adults     | 1.52 53                       | 0.53 26                         | 3.66 |
|                  | Juveniles  | 0.83 11                       | 0.36 64                         | 0.83 |
| Western          | All classes | 1.05 358                      | 0.84 415                        | 2.20 |
|                  | Adults     | 1.30 108                      | 0.88 109                        | 1.67 |
|                  | Juveniles  | 1.01 175                      | 0.83 198                        | 0.68 |
| Glaucous-winged  | All classes | 0.82 113                      | 0.65 326                        | 0.96 |
|                  | Adults     | 1.44 39                       | 0.63 49                         | 2.78 |
|                  | Juveniles  | 0.57 47                       | 0.96 155                        | 1.91 |
| Glaucous         | All classes | 1.02 133                      | 0.66 78                         | 1.82 |
|                  | Adults     | 0.64 64                       | 1.50 10                         | 0.81 |
|                  | Juveniles  | 1.25 18                       | 0.29 54                         | 5.58 |
| Great Black-backed | All classes | 0.93 27                      | 1.17 39                         | 0.04 |
|                  | Adults     | 1.00 4                        | 1.17 13                         | —    |
|                  | Juveniles  | 0.75 7                        | 0.80 9                          | —    |
| Black-legged     | All classes | 1.25 171                      | 0.79 175                        | 4.16 |
| Kittiwake        | Adults     | 1.22 82                       | 0.94 60                         | 0.36 |
|                  | Juveniles  | 1.20 33                       | 1.42 29                         | 0.00 |
| Total            | All classes | 0.97 2395                     | 0.67 3518                       | 49.99|
|                  | Adults     | 1.09 807                      | 0.74 801                        | —    |
|                  | Juveniles  | 0.81 670                      | 0.70 1206                       | 2.20 |

*P<0.05

*P<0.01
TABLE 3. Sex ratio of gulls collected from different areas.

| Gull species—Area               | All Age Classes | Adults | Juveniles |
|----------------------------------|-----------------|--------|-----------|
|                                  | Male/Female N   | χ²     | Male/Female N | χ² | Male/Female N | χ² |
| Laughing Gull                    |                 |        |             |     |             |    |
| Northeast U.S.                   | 1.42 46         | 15.50² | 0.67 10     | 10.37¹ | 2.40 17 | -  |
| Southeast U.S.                   | 1.28 137        |        | 0.88 49     |       | 1.00 8    |    |
| Central America                  | 0.47 72         |        | 1.17 13     |       | 0.88 15   |    |
| Caribbean                        | 1.90 29         |        | 4.60 28     |       | 0.00 2    |    |
| Bonaparte's Gull                 |                 |        |             |     |             |    |
| Northeast U.S. & Canada          | 1.05 133        | 3.87   | 0.79 34     | 3.21 | 1.00 60   |    |
| Southeast U.S.                   | 1.29 55         |        | 2.17 19     |       | 2.00 6    |    |
| Northwest U.S. & Canada          | 1.11 114        |        | 1.35 47     |       | 1.07 31   |    |
| California                       | 1.45 571        |        | 1.07 147    |       | 0.59 111  |    |
| Franklin's Gull                  |                 |        |             |     |             |    |
| Northern U.S. & Canada           | 1.28 107        | 0.73   | 1.21 64     | 0.83 | 1.29 16   |    |
| Southern U.S. & Central America  | 1.00 50         |        | 0.83 11     |       | 0.67 5    |    |
| South America                    | 1.04 45         |        | 0.78 16     |       | 1.60 23   |    |
| Heermann's Gull                   |                 |        |             |     |             |    |
| California                       | 0.55 513        | 4.34   | 1.00 108    | 2.68 | 0.60 154  | 2.95 |
| Mexico                           | 0.94 68         |        | 1.92 35     |       | 1.50 15   |    |
| Mew Gull                         |                 |        |             |     |             | 0.46 |
| Northwest U.S. & Canada          | 1.00 144        | 37.01² | 1.00 20     |      | 1.00 10   |    |
| California                       | 0.53 351        |        | 1.00 8      |       | 0.61 29   |    |
| Ring-billed Gull                 |                 |        |             |     |             |    |
| Eastern U.S.                     | 0.98 113        | 9.51²  | 1.25 9      | 0.61 | 1.11 19   | 4.60 |
| Western U.S. & Canada            | 0.84 61         |        | 0.85 24     |       | 0.74 40   |    |
| California                       | 0.53 402        |        | 1.24 47     |       | 0.45 145  |    |
| California Gull                  |                 |        |             |     |             |    |
| Canada                           | 0.28 37         | 0.62   | 4.00 5      |      | 0.33 4    |    |
| Northwest U.S.                   | 0.57 33         |        | 0.60 24     |       | 0.71 24   |    |
| California                       | 0.74 555        |        | 0.53 129    |       | 0.81 208  |    |
| Herring Gull                     |                 |        |             |     |             |    |
| Northeast U.S.                   | 0.91 128        | 7.94   | 1.10 21     |      | 0.77 16   |    |
| Great Lakes                      | 0.55 31         |        | 1.00 4      |       | — 0       |    |
| Southeast U.S.                   | 0.38 47         |        | — 0         |       | 0.00 3    |    |
### TABLE 3. (Continued).

| Gull species—Area          | Male/Female | N  | $\chi^2$ | Male/Female | N  | $\chi^2$ | Male/Female | N  | $\chi^2$ |
|----------------------------|-------------|----|----------|-------------|----|----------|-------------|----|----------|
| **All Age Classes**        |             |    |          |             |    |          |             |    |          |
| California                 | 0.61        | 220| 0.58     | 0.56        | 14 | 0.96     | 0.58        | 41 | 0.56     |
| Canada & Alaska            | 0.94        | 35 | 0.56     | 14          |    | 2.00     | 0.56        | 14 | 2.00     |
| **Thayer's Gull**          |             |    |          |             |    |          |             |    |          |
| Arctic                     | 1.81        | 59 | 0.50     | 18          |    | 2.00     | 0.50        | 18 | 2.00     |
| Alaska                     | 0.72        | 31 | 0.33     | 4           |    | 5.00     | 0.33        | 4  | 5.00     |
| California                 | 0.26        | 61 | 0.33     | 16          |    | 0.34     | 0.33        | 16 | 0.34     |
| **Western Gull**           |             |    |          |             |    |          |             |    |          |
| Northwest U.S.             | 0.56        | 39 | 0.75     | 7           |    | 0.20     | 0.75        | 7  | 0.20     |
| California                 | 0.91        | 625| 0.98    | 158         |    | 0.91    | 0.98        | 158| 0.91    |
| Mexico                     | 1.58        | 110| 0.95    | 43          |    | 0.50    | 0.95        | 43 | 0.50    |
| **Glaucous-winged Gull**   |             |    |          |             |    |          |             |    |          |
| Alaska & British Columbia  | 1.03        | 150| 1.63    | 43          |    | 0.81    | 1.63        | 43 | 0.81    |
| Northwest U.S.             | 0.58        | 38 | 0.63    | 26          |    | 0.56    | 0.63        | 26 | 0.56    |
| California                 | 0.54        | 249| 0.50    | 18          |    | 1.00    | 0.50        | 18 | 1.00    |
| **Glaucous Gull**          |             |    |          |             |    |          |             |    |          |
| Arctic                     | 0.84        | 153| 0.72    | 50          |    | 0.33    | 0.72        | 50 | 0.33    |
| U.S. & British Columbia    | 0.60        | 48 | 0.50    | 21          |    | 0.45    | 0.50        | 21 | 0.45    |
| **Great Black-backed Gull**|             |    |          |             |    |          |             |    |          |
| Northeast U.S.             | 1.33        | 42 | 1.17    | 13          |    | 1.00    | 1.17        | 13 | 1.00    |
| Canada                     | 0.71        | 24 | 1.00    | 4           |    | 0.00    | 1.00        | 4  | 0.00    |

1. $P<0.05$
2. $P<0.01$
a sample of 196 California Gulls discovered dead and dying inside a colony on Mono Lake, California.

Sexual differences in behavior are more likely to occur during the breeding season. Because of this, the adult sex ratio probably can be more accurately determined from specimens collected outside the breeding season. This would not be true, however, if the sexes winter in different areas and one area was more heavily sampled than the other.

We examined whether the sexes winter or migrate through different areas by segregating the data based on the season and location where each specimen was collected (Tables 2 and 3). For most species, no significant differences appeared in the sex ratio among localities or seasons. However, significant differences in sex ratios for season or location did occur in the Laughing, Mew, Ring-billed, and Glaucous-winged gulls. Consequently, sex ratio data for these species must be interpreted cautiously. The male/female ratio for Mew and Glaucous-winged gulls varied among northern and southern collecting sites, with females being more prevalent in the latter areas. This may have resulted from females migrating farther south than males.

For all these reasons, care should be exercised when interpreting the results of any study on the sex ratio of an avian population. The results of this study are no exception. We cannot entirely rule out the possibility that our results are biased and that the sex ratios of museum specimens may not be the same as the populations from which the specimens were drawn. But this is true for any sex ratio study of a free-ranging avian species. The best solution to this problem is to test for biases as we have done in this study and to compare the results of studies which have used different collecting techniques. Confidence can only be obtained when different investigators using different experimental techniques reach similar conclusions.

Interspecific Differences

One interesting finding of this study is that the sex ratios of the black-headed and white-headed gulls differed substantially from each other. In all three black-headed gull species, females significantly outnumbered males among prefledglings but the opposite was true among adults.

In the white-headed gulls, the sex ratio of prefledglings in all species was even but among the first-year birds, females significantly outnumbered males in most of the species under study. Males, however, became more numerous in the older age classes and significantly so in _L. marinus_. It is unclear what accounts for these differences between the black-headed and white-headed gulls or even if these observed differences are real or the result of some bias in the data. One possibility is that sexual variation in parental roles and reproductive behavior may result in higher mortality in one sex than the other. Alternatively, female black-headed gulls,
among the smallest of the North American gulls, possibly suffer a competitive disadvantage during the winter, being easily excluded from food sites by larger gulls. Understanding of these findings must await the completion of other studies.

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**Literature Cited**

Altman, S. A., S. S. Wagner, and S. Lenington. 1977. Two models for the evolution of polygyny. Behavioral Ecology and Sociobiology 2: 397-410.

Burger, J. 1983. Determining sex ratios from collected specimens. Condor 85: 503.

Burger, J., and M. Gochfeld. 1981 Unequal sex ratios and their consequences in Herring Gull (Larus argentatus). Behavioral Ecology and Sociobiology 8: 125-128.

Conover, M. R. 1984. Frequency, spatial distribution and nest attendants of supernormal clutches in Ring-billed and California gulls. Condor 86: 467-471.

Conover, M. R. and G. L. Hunt Jr. 1984a. Female-female pairing and sex ratios in gulls: a historical perspective. Wilson Bulletin 96: 619-625.

Conover, M. R. and G. L. Hunt Jr 1984b. Experimental evidence that female-female pairs in gulls result from a shortage of breeding males. Condor 86: 472-476.

Conover, M. R., D. E. Miller, and G. L. Hunt Jr. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California gulls. Auk 96: 6-9.

Dwight, J. 1925. The Gulls (Laridae) of the world; their plumages, moult, variations, relationships and distribution. American Museum of Natural History Bulletin 52: 62-408.

Fitch, M. A. 1980. Monogamy, polygamy and female-female pairs in Herring Gulls. Proceedings of the Colonial Waterbird Group 3: 44-48.

Hunt, G. L. Jr., and M. W. Hunt. 1977. Female-female pairing in Western Gulls (Larus occidentalis) in southern California. Science 196: 1466-1467.

Hunt, G. L. Jr., M. W. Hunt, J. C. Wingfield, A. Newman, and D. S. Farner. 1980. Sex ratio of Western Gulls on Santa Barbara Island, California. Auk 97: 473-479.

Jehl, J. R. Jr. 1987. Geographic variation and evolution in the California Gull (Larus californicus). Auk 104: 421-428.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103: 589-603.

Ryder, J. P. and P. L. Somppi. 1979. Female-female pairing in Ring-billed Gulls. Auk 96: 1-15.

Sayce, J. R. and G. L. Hunt, Jr. 1987. Sex ratios of pre-fledging Western Gulls. Auk 104: 33-37.

Shugart, G. W. 1981. Frequency and distribution of polygyny in Great Lakes Herring Gulls in 1978. Condor 82: 426-429.

Shugart G. W., and W. E. Southern. 1977. Close nesting a result of polygyny in Herring Gulls. Bird-Banding 48: 270-277.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18: 253-263.

Verner, J. and M. F. Wilson. 1966. The influence of habitat on mating systems of North American passerine birds. Ecology 47: 143-147.