

SEX RATIO OF WESTERN GULLS ON SANTA BARBARA ISLAND, CALIFORNIA

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ABSTRACT.—Female-female pairs constituted at least 10%, perhaps a substantially greater fraction, of the 1972–1978 breeding population of Western Gulls (*Larus occidentalis*) on Santa Barbara Island, California. In this population, the adult sex ratio was estimated to be 0.67 males per female. This appears to be the consequence of differential survival rates and may have a causal role in the formation of female-female pairs. *Received 25 June 1979, accepted 31 December 1979.*

FEMALE-FEMALE pairing among Western Gulls (*Larus occidentalis*) on Santa Barbara Island, California may be a response to an excess of breeding-age females (Hunt and Hunt 1977). Unpaired, these females are unable to rear young, because the efforts of two adults are essential for protection and incubation of the clutch and for rearing of the young (Hunt pers. obs. but see Nisbet et al. 1978). Members of female-female pairs that copulate with promiscuously breeding males, however, produce fertile eggs and can rear young by sharing parental functions. The not mutually exclusive hypothesis that female-female pairs may result from hormonal masculinization has also been tested and is the subject of another communication. In this paper we present additional data that are consistent with the hypothesis that the sex ratio in this colony of Western Gulls is strongly skewed in favor of females and preliminary evidence that the sexes may have different survival rates.

MATERIALS AND METHODS

Adult and subadult Western Gulls were captured in 1977 and 1978 with baited and unbaited cannon-net shots at "loafing" sites ("clubs") in nonterritorial areas, with baited "walk-in" traps in nonclub areas, and with nooses at nests. Chicks were captured on their territories prior to fledging and varied in age from 5 to 40 days.

Cannon-netting and trapping were conducted from mid-March through late June in both years. Cannon-netting was conducted usually before 0900 or after 1600, as these were periods when larger numbers of birds were present in clubs and there was less chance of captured birds overheating. The "walk-in" traps were used at all times of day with the exception of days when the ambient temperature rose above 30–35° C. In 1977, the sex of captured birds was determined by unilateral laparotomy (a surgical technique whereby the gonads and their ducts are visually examined) or by size. Table 1 gives means and standard deviations of several characters by which males and females can be separated. Although males are larger than females in all of these characters, the smallest males were exceeded by 22% of the females in weight, 61% in bill length, 52% in bill depth, and 8% in head plus bill length. Therefore, initially in 1977, the largest males and smallest females were sexed on the basis of size, and intermediate sized birds were sexed by laparotomy. After the beginning of the breeding season of 1977 and in 1978, however, sex was determined solely by laparotomy. This method assured complete accuracy and also allowed us to determine the stage of gonadal development at the time of capture. No mortality could be related to this sexing method and less than a 5% desertion rate was detected. All gulls were marked with numbered leg bands from the U.S. Fish and Wildlife Service and with individually distinctive combinations of colored bands.

Breeding condition and reproductive status were determined from the condition of the gonad and from observations of the behavior throughout the breeding season of individuals color-banded at the time of laparotomy. A female was considered to be breeding if the ovary contained a follicle with a diameter

TABLE 1. Size differences of male and female Western Gulls captured on Santa Barbara Island, 1975–1976.

| | Males $\bar{x} \pm SD$ | Females $\bar{x} \pm SD$ | <i>z</i> | <i>P</i> |
|------------------------------|---------------------------|-----------------------------|----------|----------|
| Sample size | 28 | 73 | | |
| Weight (g) | 982 \pm 56.8 | 769 \pm 43.1 | 17.96 | <0.01 |
| Bill length (cm) | 5.58 \pm 0.24 | 5.08 \pm 0.22 | 9.59 | <0.01 |
| Bill depth ^a (cm) | 2.12 \pm 0.12 | 1.91 \pm 0.06 | 8.85 | <0.01 |
| Head plus bill length (cm) | 12.79 \pm 0.27 | 11.75 \pm 0.20 | 18.53 | <0.01 |

^a At deepest point.

greater than 5 mm, if the oviduct was enlarged (the magnum greater than 3 mm in diameter), or if an incubation patch had developed. In males, the size of the testes alone could not be used as an indicator of breeding status, because nonbreeding birds may have enlarged testes; behavioral criteria and the presence of an incubation patch were also used. For both males and females, behavioral criteria for "breeding" status included: (1) three or more observations on separate days in the same territorial area with no conflicting observation of territorial behavior elsewhere, (2) capture while incubating or feeding chicks, or (3) three or more observations on separate days of harrasing intruders in the same area. Territorial behavior included presence in a portion of the colony near a nest, with or without a mate; defense of a territory; and incubation or chick care. Failed breeders of both sexes were considered as breeders because they were paired, held territory, and attempted to nest. Anatomical and behavioral assessments of reproductive status were generally in agreement when adequate data of both types were available.

Nonbreeding females were identified by the presence of small (<2 mm in diameter) ovarian follicles, some of which were atretic, and the absence of a complete incubation patch after the mean period of egg laying for the colony. For males, nonbreeders were identified by the absence of an incubation patch after the period of egg laying. Behavioral criteria for "nonbreeding" status (in birds captured before the egg-laying period and observed thereafter but without recapture) included: three or more observations in a club with no sightings on a territory prior to June, three or more observed evictions from a territory, three or more observations on different territories, or a combination of the latter two. Birds that could not be assigned status on the basis of these criteria were eliminated from the analyses related to breeding status.

Age was determined on the basis of plumage characteristics and, in a few cases, on the basis of banded birds of known age. Birds with no black in the tail and a clear red spot on an otherwise yellow bill were classified as adult.

RESULTS

In 1977 and 1978, the sex of 1,060 Western Gulls was determined; ages ranged from 1 week to fully adult (Table 2). The sex ratio of the adult population appeared heavily skewed in favor of females. The 2- and 3-year-old birds captured also exhibited an excess of females, but, like the sex ratio of 4- and 5-yr-old birds, this ratio was not significantly different from 1.0 (4 and 5 yr, $\chi^2 = 0.22$, *df* = 1, *P* > 0.05; 2 and 3 yr, $\chi^2 = 1.59$, 1 *df*, *P* > 0.05). The sex ratio of chicks, while skewed in favor of females, also was not significantly different from 1.0 ($\chi^2 = 1.51$, *df* = 1, *P* > 0.05). The adult sample included a small number of females that had been noosed at the nests of female-female pairs, thereby creating a bias toward females. When these noosed birds were excluded, the sex ratio of captured adult birds was 0.26 and 0.25 males per female for 1977 and 1978, respectively.

Such a large excess of females seems unreasonable. Most birds on the island are paired, and we have estimated female-female pairs make up only 10–15% of the population (Hunt and Hunt 1977). It is possible that females are easier to catch, either because they spend more time on the island (A. Newman, M. H. Warner, G. L. Hunt, and J. C. Wingfield MS) or because they are more readily attracted to a

TABLE 2. Sex ratios of Western Gulls captured on Santa Barbara Island.

| Age | 1977 | | | | 1978 | | | | 1977 + 1978 | |
|------------------|------------|------|--------------|------|------------|------|--------------|------|--------------|------|
| | Cannon-net | | All captures | | Cannon-net | | All captures | | All captures | |
| | <i>n</i> | ♂/♀ | <i>n</i> | ♂/♀ | <i>n</i> | ♂/♀ | <i>n</i> | ♂/♀ | <i>n</i> | ♂/♀ |
| Adults | 274 | 0.26 | 300 | 0.25 | 125 | 0.15 | 306 | 0.26 | 606 | 0.26 |
| 4- and 5-yr-olds | 73 | 1.09 | 73 | 1.09 | 77 | 0.67 | 91 | 0.82 | 164 | 0.93 |
| 2- and 3-yr-olds | 20 | 0.67 | 20 | 0.67 | 28 | 0.75 | 31 | 0.72 | 51 | 0.70 |
| Chicks | — | — | 239 | 0.85 | — | — | — | — | 239 | 0.85 |

baited net. It is also possible that a significant fraction of the nests of female-female pairs contained only three eggs and were therefore not identified as such, since in past we have captured female-female pairs incubating 3-egg clutches. In 1978, a poor year for reproduction in the colony, 17 of 28 nests that in previous years had supernormal clutches had 3 or fewer eggs.

Most cannon-net shots were baited with popcorn to attract the maximum number of birds in the colony to the net. In 1977, however, we made two unbaited cannon-net shots on clubs in May to obtain an unbiased estimate of the sex ratio of birds resident in clubs. We captured 16 adult females and two adult males. Among the immature birds, we captured six males and five females. If we assume a 1977 population of 896 breeding pairs, up to 15% of which are female-female pairs (Hunt and Hunt 1977), and a nonbreeding population of at least 200 adults on the clubs with a sex ratio of 0.13, we then estimate the true sex ratio of adults on the island at 784 males to 1,209 females, or 0.67. This is similar to the sex ratio of captured 2- and 3-yr-old birds (Table 2).

There is indirect evidence that there are fewer males than females in the breeding population. Of the adults captured, 65% of the males were identified as breeding, in contrast to only 48% of the females (Table 3). Conversely, there were more adult female nonbreeders than nonbreeding males. We also found more breeding males than females in subadult plumage (Table 3). These observations suggest that there was deficit of adult males in the population.

Preliminary data on the return of the two sexes to the colony from one year to the next, based on resighting in 1978 of birds banded in 1977, are given in Table 4. Females appear to have a slightly higher return rate than males. The difference is statistically significant only when all age classes are considered together. We must await the results of band returns from individuals of known sex to be certain that these results reflect differences in survival and not sex-biased differences in philopatry.

TABLE 3. Breeding status of Western Gulls, 1977 + 1978.

| Age class | Breeding | Not breeding | Uncertain ^a | <i>P</i> ^b |
|-------------------------|----------|--------------|------------------------|-----------------------|
| Adult males | 109 | 2 | 57 | <0.005 |
| Adult females | 330 | 54 | 304 | |
| 4- and 5-yr-old males | 13 | 4 | 91 | <0.005 |
| 4- and 5-yr-old females | 1 | 8 | 101 | |

^a Large numbers of birds were classified with an uncertain breeding status because anatomical criteria were not met and we obtained too few observations or contradictory observations to permit classification on the basis of behavior.

^b Chi-square using only birds of known status.

TABLE 4. Return rates of Western Gulls, 1977-1978, Santa Barbara Island.

| Age class | <i>n</i> in 1977 | | Percent returning, 1978 | | <i>P</i> ^a |
|------------------|------------------|---------|-------------------------|---------|-----------------------|
| | Males | Females | Males | Females | |
| All birds | 105 | 286 | 69 | 78 | <0.05 |
| All adults | 59 | 239 | 71 | 79 | <0.25 |
| Breeding adults | 40 | 111 | 80 | 90 | <0.10 |
| 4- and 5-yr-olds | 38 | 35 | 71 | 71 | <0.25 |
| 2- and 3-yr-olds | 8 | 12 | 38 | 78 | <0.10 |

^a *P* values based on chi-squared test comparing numbers of birds returning and not returning in each age category.

DISCUSSION

At the outset of this study, we hypothesized that, if the female-female pairs of Western Gulls were forming in a population with a sex ratio of unity, there should then be a large excess of males in the clubs. Conversely, if the sex ratio in the population were skewed in favor of females, there should be either similar numbers of males and females or an excess of females in the clubs. The data (Tables 2 and 3) are inconsistent with the first hypothesis but provide strong evidence of a population heavily skewed toward an excess of females.

The probable sex ratio of the population on Santa Barbara Island is not greater than 0.67 males per female. Greater precision is not possible because of probable differences in daily patterns of activity between males and females and because of possible differences between the sexes in attraction to baits. This ratio, however, provides a minimum estimate of the bias in sex ratio among gulls attempting to breed at Santa Barbara Island. Because populations away from the island are influenced by events on the island in the breeding season, and because migrants augment the southern California population at other seasons, there appears to be no way to refine this estimate further at present. Eventually, data on differential survival of chicks of known sex will resolve this question for the population.

Little information is available on the sex ratios of other populations of gulls. A similar excess of females has been shown for Red-billed Gulls (*L. novaehollandiae*, Mills 1973). Goethe (1937), however, reported a secondary sex ratio of 1.06 males per female in a breeding population of the Herring Gull (*L. argentatus*) in Germany. In general, one expects a ratio of approximately 1.0 in monogamous species of birds (Fisher 1930), and in most populations that have been examined such a ratio or a modest excess of males has been reported. In contrast, polygamous species may have an excess of females in the adult population (Trivers 1972), but polygyny also occurs in many species with an adult sex ratio of 1.0 (Wittenberger 1976).

Most if not all species of gulls are primarily monogamous, recent observations of polygyny by Shugart and Southern (1977) and Conover et al. (1979) notwithstanding. It would appear that there would be little selective advantage in producing an excess of females that would be unable to produce young. The somewhat smaller female gulls, however, may be energetically less expensive to raise (G. L. Hunt unpubl. data). Applying the arguments of Fisher (1930) and Trivers (1972), one might then expect an excess of females at fledging, especially if the availability of food to breeding birds is limited in this stable or declining gull population (Myers 1978, Hunt et al. 1979).

The slight excess of females in pre-fledging chicks may reflect a difference in investment in the sexes, but additional data are necessary to test this hypothesis. If

the posthatching mortality rates of females were formerly higher than those of males due to competitive exclusion (by males) of females from scarce trophic resources, then an excess of females at the end of the period of parental care might have resulted ultimately in a balanced sex ratio. With excess waste food from contemporary human civilization available as a trophic resource, the original cause of postfledging female mortality may have been reduced.

An alternative hypothesis is that changes in the behavior or ecology of males 12–15 yr ago, when supernormal clutches were first noted for Western Gulls (Schreiber 1970), has resulted in increased male mortality. Assuming that the widespread and long-noted presence of supernormal clutches in Ring-billed Gulls (*L. delewarensis*) associated with female-female pairing is also the result of a skewed sex ratio (Hunt and Hunt 1977, Ryder and Somppi 1979, Conover et al. 1979), however, a recent local change in male mortality in Western Gulls seems unlikely.

Coulson and Wooller (1976) have examined differences in survival rates by sex and age class in the Black-legged Kittiwake (*Rissa tridactyla*) in northern England. In this 21-yr study they found that females enjoyed a higher annual survival rate than males (0.86 vs. 0.81) and that the difference between the sexes was greatest in years in which the total survival rate was low. Although a small pelagic gull like the kittiwake has a life history and ecology very different from that of the Western Gull, annual survival rates for the two sexes are remarkably similar to return rates found for breeding adults in the present study (females, 0.90; males, 0.80). Coulson and Wooller found that the higher mortality of males relative to females occurs in spring, when males are reestablishing territories and courting, and is more pronounced in the center of the colony than at its edge. This finding does not support the hypothesis that the cause of differential survival of males and females is trophic. Likewise, Chabrzyk and Coulson (1976) failed to find evidence of differential survival of the sexes in Herring Gulls.

Coulson and Wooller (1976) do not mention a skewed sex ratio in the kittiwake population, despite a 0.05 difference in survival between males and females. Coulson (in litt.) reported that the adult breeding sex ratio was close to unity with a slight excess of females. If the population were as closed as they believe, one might have expected an excess of females. Likewise, Chabrzyk and Coulson (1976) found a sex ratio of unity in adult Herring Gulls, although more females than males emigrate to new colonies to begin breeding. Presumably, such movement among colonies balances out. In the Channel Islands of California, supernormal clutches have been found on all islands, so we assume that this entire population has an excess of females.

When sex ratios are unbalanced, the rarer sex may mate at an earlier age (Wittenberger 1980). Thus, in populations of Red-billed Gulls with an excess of females, females have difficulty in finding mates, and males mate at an earlier age (Mills 1973). In the Black-legged Kittiwake, in which differences in mortality rates in a closed population suggest that there should be an excess of females, males mate for the first time about 1 yr earlier than females (Coulson and Wooller 1976). A similar situation was found in Adelie Penguins (*Pygoscelis adeliae*) by Ainley (1978). In contrast, Richdale (1957) has reported an excess of males in a population of Yellow-eyed Penguins (*Megadyptes antipodes*) in New Zealand in which females breed at an earlier age.

If a population is expanding, there may not be a nonbreeding excess of the more common sex. If a population is in a steady state or declining, however, there may

be adult individuals of the more common sex that are unable to mate, even though they would accept younger individuals of the rarer sex. Thus, in the Red-billed Gulls studied by Mills (1973) and the Black-legged Kittiwakes studied by Coulson and Wooler (1976), the populations had been recently or still were expanding, and no excess of unmated adult females was reported. In contrast, the Western Gull population on Santa Barbara Island has been stable or declining (Hunt et al. 1979) and there is an excess of non-breeding adult females.

Ryder (1978) has suggested that excess male mortality early in the breeding season might result in fertilized females being forced to mate with another fertilized, widowed female, because these females would have insufficient time, due to the proximity of egg laying, to form a pair bond with a male. At least in Western Gulls, considerable evidence indicates that this hypothesis is untenable. Female-female pairs form well before egg laying commences (A. Newman, M. H. Warner, G. L. Hunt, J. C. Wingfield MS; unpubl. obs.), female-female pairs remain together from one year to the next (Hunt and Hunt 1977), most eggs produced by female-female pairs are infertile (Hunt and Hunt 1977), and there is no evidence of a sudden upsurge of male mortality between the beginning of copulations on the colony and egg laying (obs. made during this study). Female-female pair formation may take place in the manner suggested by Ryder (1978) in Ring-billed Gulls, in which fertility in supernormal clutches is high (Ryder and Somppi 1979, Conover et al. 1979), but no supporting evidence is available.

Very little has been published on female-female or male-male pairings in birds (Hunt and Hunt 1977, Ryder and Somppi 1979, Conover et al. 1979). The few cases reported in the literature prior to the recent observations on gulls have all involved homosexual pairing in captive or domestic birds held in groups with highly skewed sex ratios (Collias and Jahn 1959; Dilger 1960; Slater, in Jefferies 1967; Sauer 1972). Additionally, a number of aviculturalists have informed us of the occurrence of homosexual pairings in otherwise heterosexual individuals when the populations involved are segregated by sex. Thus, it is reasonable to assume that homosexual pairings may occur in a wild population because of a skewed sex ratio, as in the population of Western Gulls on Santa Barbara Island. We now need experimental tests to demonstrate this assumed relation between sex ratio and homosexual matings, as well as information on the cause and temporal course of the development of the skewed sex ratio. Finally, these homosexual pairs raise a number of interesting questions concerning how courtship patterns, evolved for selection of a high-quality mate of the opposite sex (Wittenberger 1976, Orians 1969), permit homosexual mating, the skewed sex ratio of the population notwithstanding.

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