Origin of Homosexual Pairing of Female Western Gulls on Santa Barbara Island

John C. Wingfield,[1] Audrey Martin,[2] Molly W. Hunt,[2]
George L. Hunt, Jr.,[2] and Donald S. Farner[1]
[1]*Department of Zoology, University of Washington,*
Seattle, Washington 98195
[2]*Department of Ecology and Evolutionary Biology,*
University of California, Irvine, California 92717

INTRODUCTION

In 1968, Schreiber (1970) found that 11.3 per cent of the clutches of Western Gulls (*Larus occidentalis wymani*) on San Nicolas Island had more than three eggs. He believed that the low hatching success (0.13 per cent) of these clutches was the result of insufficient heat transfer in incubating four or more eggs. On Santa Barbara Island in 1972, 11 per cent of clutches were found to consist of more than three eggs, with 4.9 per cent hatching success (Hunt and Hunt 1973). It was believed, at first, that these eggs all came from the same female, as the eggs were of similar color and only two adults could be identified on each territory. Between 1972 and 1976, the frequency of clutches with supernumerary eggs varied between 7 and 13 per cent. It also became apparent that these were laid by female-female pairs.

Evidence for female-female pairing found by Hunt and Hunt (1977) is as follows:

(1) In three-egg clutches, 67 per cent of eggs were laid two days apart, whereas in the larger clutches many were laid on consecutive days and 11 per cent on the same day. This suggests that at least two females were laying in the same nest.

(2) Most eggs in the clutches with more than three eggs were infertile. While 81.5 per cent of the eggs of normal clutches showed development, zero to 14 per cent developed in the larger clutches. The few eggs that were fertile resulted from promiscuous, heterosexual matings. Indeed, marked birds have been observed mounting or being mounted by birds other than their mate. In such situations males were off their own territory, and in five of 18 cases females were also off their own territory.

(3) The sex of gulls trapped on nests perhaps provides the most convincing evidence. Hunt and Hunt (1977) trapped 10 male and 15 female adult gulls incubating normal clutches (one to three eggs), and one male and 74 females on larger clutches. Most important, on 23 nests containing larger clutches, two females were captured.

Thus, it appears that on territories where nests contained large clutches, two females are in attendance with no apparent permanent association of males for at least one to two weeks prior to clutch initiation. These females essentially act as though they are heterosexually paired and remain together from one year to the next, although in one instance a female paired to another female in 1976 was found paired to a male in 1977. They engage in most of the usual courtship and territorial behavior but relatively rarely show mounting and copulation behavior normally attributable to males. If given hatching eggs, they are capable of raising young (G. Hunt, M. Hunt, and S. Anthony, unpubl. field notes).

The existence of female-female pairs raises many questions. If the quality of a mate is assessed in courtship, how is the mechanism failing, and how widespread and important is promiscuous, heterosexual mating? Why do female-female pairs form? For the last question we have two working hypotheses, which are not mutually exclusive. These hypotheses are the subject of this paper.

TABLE 1. Sex ratios of Western Gulls caught by cannon-net, 22 April-5 May 1977, and of newly-hatched chicks on Santa Barbara Island.

	Females	Males	Female/male	P[1]
All adults	108	46	2.35	<0.005
All immatures	31	25	1.24	>0.05
Breeding adults[2]	88	45	1.95	<0.01
Nonbreeding adults	20	1	20.00	<0.005
Breeding immatures[3]	2	16	0.13	<0.05
Nonbreeding immatures	29	9	3.22	<0.05
Newly-hatched chicks	129	110	1.17	<0.05

[1] χ^2-test for equality of the sexes.

[2] Difference in the percentage of nonbreeders in adult males and females significant at $P<0.01$.

[3] Difference in the percentage of nonbreeders in immature males and females significant at $P<0.005$.

WHY DO FEMALE-FEMALE PAIRS FORM?

The first hypothesis is that the sex ratio is biased in favor of females, thus resulting in female-female pairing owing to a shortage of males. The homosexual pairs formed would have a small chance of raising young (owing to promiscuous, heterosexual matings), whereas an unmated female would have essentially no chance since she would be unable to raise young alone. We have tested the hypothesis that there is a bias in the sex ratio by cannon-netting Western Gulls in "clubs" on Santa Barbara Island during the 1977 breeding season and sexing them by unilateral laparotomy. The breeding status of birds was determined by inspection of the gonads and through the observation of the marked birds following their release after the laparotomy. Results are presented in Table 1, and it appears that there is, indeed, a skewed sex ratio in favor of females. In nonbreeding adults, females outnumbered males twenty to one. In addition, four- and five-year-old birds breeding for the first time were mostly males. These data are consistent with the hypothesis that there is a shortage of males in the breeding population. However, this is the first study of sex ratio in a gull colony, and it is not known if such a biased ratio is unusual. A similar study of a colony with no, or very few, clutches with more than three eggs may resolve this problem. We attempted to determine whether the apparent bias in the sex ratio of the adults originated before or after hatching by sexing newly-hatched chicks. A total of 249 chicks were sexed by laparotomy in 1977 and, although there was an excess of females (Table 1), the difference between the ratio found and a 1:1 ratio was not statistically significant.

The second hypothesis is that female-female pairing is a result of modification of behavior by abnormal plasma hormone levels or cycles. To test this hypothesis, we collected blood samples from both males and heterosexual and homosexual females throughout a breeding season on Santa Barbara Island. Blood was taken from a wing vein using heparinized syringes and was centrifuged in the field using a clinical centrifuge powered by a portable generator. Plasma was stored frozen in a liquid nitrogen refrigerator and transported to Seattle for analysis. Luteinizing hormone, a protein secreted by the pituitary gland and transported via the blood to its target organ, the gonad, was measured by a double antibody radioimmunoassay (Follett *et al.* 1972). The primary effects of this hormone are on the interstitial cells of both the testis and the ovary, and also on the thecal cells of ovarian follicles, causing them to synthesize and secrete sex steroid hormones (Brown *et al.* 1975, Lofts and Murton 1973). Of these steroid hormones,

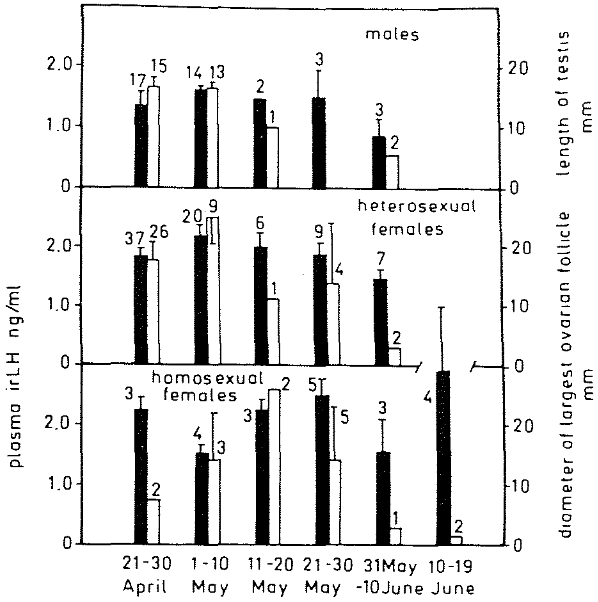

FIGURE 1. *Plasma levels of immunoreactive luteinizing hormone (dark bars) and gonadal size (open bars) in relation to calendar time. Fine bars are standard errors of means. Numbers above bars indicate sample sizes.*

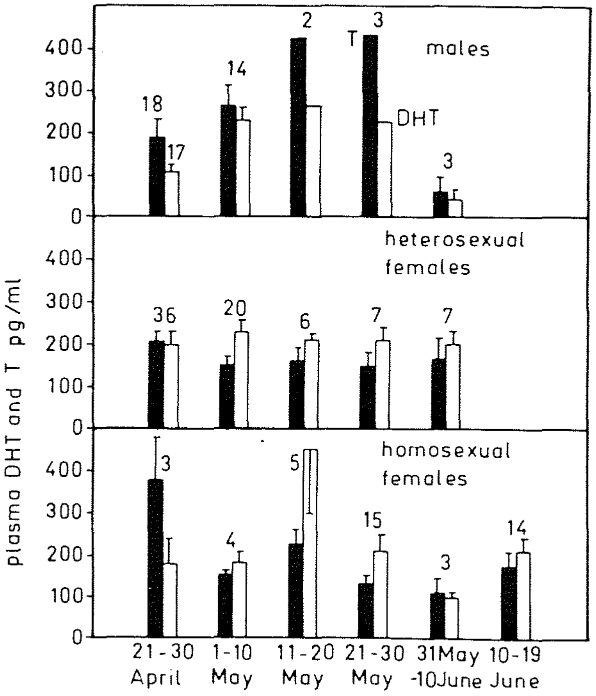

FIGURE 2. *Plasma levels of 5αDHT (open bars) and testosterone (dark bars) in relation to calendar time. Fine bars are standard errors of means. Numbers above bars indicate sample sizes.*

progesterone, 17β-hydroxy-5α-androstan-3-one (5α-DHT), testosterone, estrone, and estradiol-17β were again measured by radioimmunoassay (Wingfield and Farner 1975). The actions of these hormones include control of gametogenesis, secondary sex characteristics, and reproductive behavior (see Lofts and Murton 1973 for review).

Figures 1 and 2 summarize the plasma levels of immunoreactive luteinizing hormone (irLH), gonadal size, plasma 5α-DHT, and testosterone in relation to calendar time. Very little change was seen in females; however, in males, androgen (5α-DHT and testosterone) levels were highest during the peak period of egg laying (May), with lower levels during incubation. As females in May were either about to lay, in lay, or incubating eggs, the data were rearranged according to stages in the cycle, rather than by calendar time (Fig. 3), in order to clarify the relationship between hormone levels and the reproductive cycle. As can be seen, there is a peak in plasma irLH at ovulation in heterosexual females, as has been shown in other species (Furr *et al.* 1973, Donham *et al.* 1976, Wingfield and Farner 1978). The small sample sizes in homosexual females prevent us from making comparisons except for the period of incubation. During incubation, plasma irLH rises in homosexually paired females, whereas a decrease was noted at this time in heterosexual females. Cheng and Follett (1976) found that plasma irLH remained elevated in female Ring Doves incubating infertile eggs compared with those incubating fertile eggs. This they related to renesting attempts by females having infertile eggs. As homosexual gulls are incubating mainly infertile eggs, it is tempting to draw a parallel with Ring Doves even though, to date, none of these females has been recorded as renesting.

From Figure 3 it can also be seen that plasma androgen levels show a maximum at or near ovulation in heterosexual females and that the absolute levels in males and females are remarkably similar (Fig. 2). The ratio of androgen in male plasma to that in female plasma barely exceeds two, whereas in other wild species studied, such as the White-crowned Sparrow, *Zonotrichia leucophrys* (Wingfield and Farner 1978), and the Mallard, *Anas platyrhynchos* (R. S. Donham, pers. comm.), the ratio lies between ten and twenty to one. This difference may be related to the behavior of these species. Male White-crowned Sparrows and Mallards are mainly responsible for territorial defense, and, in the Mallard, the male has no parental responsibilities at all. In the Western Gull, territorial defense and parental duties are more or less equally divided.

Measurements of plasma progesterone, estrone, and estradiol-17β are not yet complete, but preliminary data show apparent maxima in all hormones in females during egg laying. As these hormones have been implicated in the control of vitellogenesis and ovulation, such maxima are to be expected (see Lofts and Murton 1973). Changes , if any, in levels of these hormones in the plasma of males are at present unclear.

From our very preliminary data on hormone levels we can tentatively conclude that plasma androgen and irLH are present at similar concentrations in both males and females. As these hormones are thought to regulate territorial and sexual behavior, and given the fact that females display many behavioral traits normally attributable to males, it is not difficult to rationalize the formation of female-female pairs in a population with a shortage of males. The fate of these "absent" males is at present unknown.

SUMMARY

Clutches of four to six eggs have been found in seven to 13 per cent of Western Gull (*Larus occidentalis wymani*) nests on Santa Barbara Island. Evidence that these larger clutches are the product of female-female homosexual pairings is reviewed and new evidence related to two working hypotheses on the origin of these pairs is presented.

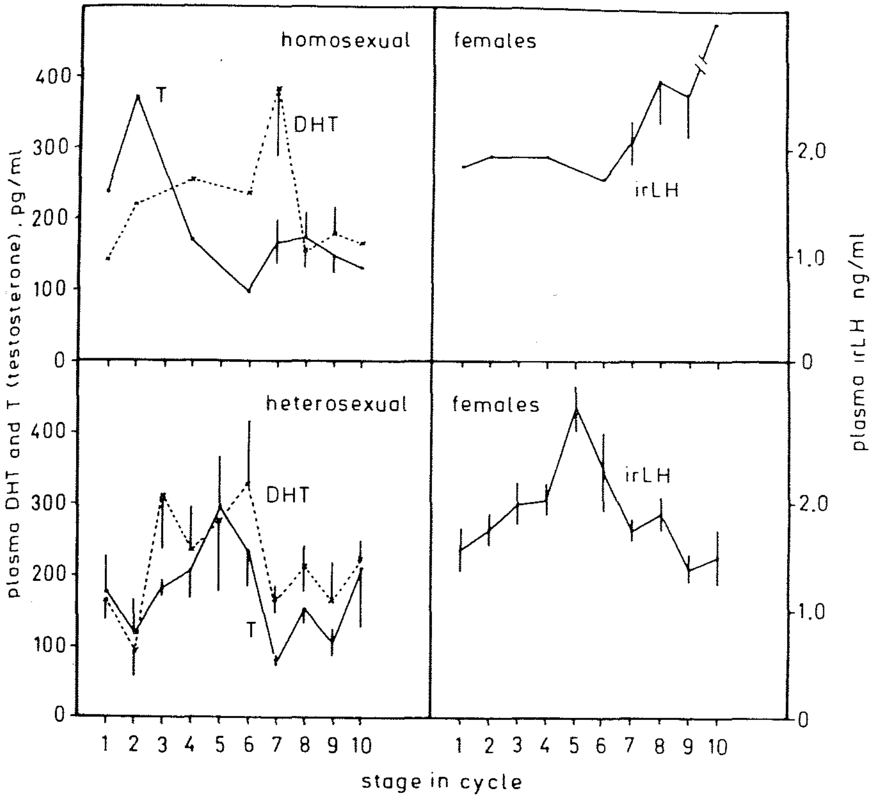

FIGURE 3. *Plasma levels of immunoreactive luteinizing hormone and androgen (± standard errors of means) in relation to stage in cycle. Key to stage numbers is as follows: (1) largest ovarian follicle, 5 mm; (2) largest ovarian follicle, 10 mm; (3) largest ovarian follicle, 15 mm; (4) largest ovarian follicle, 30 mm; (5) largest ovarian follicle > 30 mm, about to ovulate; (6) egg in oviduct; (7) very early incubation; (8) mid-incubation; (9) late incubation; (10) feeding chicks.*

One hypothesis, that female homosexual pairing is associated with a skewed sex ratio, has been examined by cannon-netting adults in loafing areas or "clubs" on Santa Barbara Island. We have caught more adult females than males, and found a higher proportion of nonbreeding adult females than males. Among subadult gulls caught, a higher proportion of males was found breeding than females. These data are consistent with the hypothesis that there exists an excess of adult female gulls on Santa Barbara Island; we have no information suggesting the cause of the skewed sex ratio. However, in a population with a predominance of females, female homosexual matings would be favored, if birds so paired could raise young resulting from promiscuous, heterosexual mating. Unpaired females have almost no chance of leaving offspring.

A second hypothesis, not mutually exclusive with the first, is that female-female pairs are the result of abnormal hormonal cycles modifying behavior. This is being tested by quantitative measures of behavior and of plasma levels of hormones. Both homosexually and heterosexually paired females show some behavioral patterns normally attributable to males. It is presently unclear whether there are significant hormonal differences between homosexually and heterosexually mated females.

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Nesting Success of Western Gulls on Bird Rock, Santa Catalina Island, California

Judith L. Hand

Biology Department, University of California,
Los Angeles, California 90024

INTRODUCTION

In 1965 and 1966, Charles Harper studied aspects of reproductive biology in a colony of less than thirty pairs of Western Gulls *(Larus occidentalis wymani)* on Bird Rock, a small islet approximately 530 m off the east side of the isthmus at Santa Catalina Island, California (Harper 1971). In 1974, I made observations on breeding success at Bird Rock which were comparable to some of the data reported by Harper. This paper presents results of comparison of the two studies.

STUDY SITE AND METHODS

Bird Rock is roughly oval and dome shaped, about 135 m long by 90 m wide. For the most part, the hard surface is smooth and bare with few fissures or prominent contours. A low-growing patch of vegetation ringed by prickly pear cactus *(Opuntia occidentalis)* covers part of the southwest end.

With the exception of a pair of Killdeer *(Charadrius vociferus)* found on 22 June 1975, I saw no other vertebrates on the island. Harper noted a breeding pair of Black Oystercatchers *(Haematopus bachmani)* in 1966 and occasional sea lions *(Zalophus californianus)* resting on the island, but otherwise he also saw no other vertebrates. The Killdeer seen in 1975 performed impressive distraction displays on the south end of the island, suggesting that they were nesting or intended to nest there, but my superficial hunt did not detect the nest. It may have been within the border of the vegetation patch.

The highest part of the islet forms a ridge that runs lengthwise across the top and middle and separates the northeast and southwest slopes. The gulls do not nest on the northeast side, probably because the surface is too steep. Nests are found primarily along the ridge and over the face of the southwest slope (Fig. 1).

The area around Bird Rock is used extensively for human recreation. Access to the islet itself is hindered to some extent because the intertidal zone has numerous jagged rocks and there is always considerable swell, even in calm weather. Difficulties in getting onto the islet, plus its barren and uninteresting appearance, have probably contributed significantly to continued occupation of the gull colony in spite of heavy human traffic in the area. Nevertheless, Harper reported significant mortality in both 1965 and 1966 which he attributed to human disturbances.

Harper visited the colony six times each season, at roughly two-week intervals, beginning in late May and continuing through July. At each visit he counted numbers of nests, eggs, and chicks present. Nests were labeled by painting numbers next to them on the rock. Chicks were banded with temporary bands when about twenty days old.

I made a census of the colony three times in 1974, on 12 May, 19 May, and 13 July. This was sufficient to collect data on nest locations, clutch sizes, and probable hatching success which are comparable to the data collected by Harper. Nests were identified by numbers painted on the rock. Individual eggs and chicks were not marked.

I made no visits during the weeks following completion of clutches or following hatching, so