

Female-Female Pairing in Western Gulls
(Larus occidentalis) in Southern California

Abstract. Pairs of females that remain together from one year to the next are associated with the presence of supernormal clutches in western gull nests. Intervals between laying of eggs in supernormal clutches are less than those found in normal clutches, a result indicating both females in a pair contribute to the clutch. Most eggs in supernormal clutches are infertile. The pairs of females occupy territories that are not shared with a resident male. In three homosexual pairs one of the females exhibited behaviors normally ascribed only to males.

Supernormal clutches (four to six eggs) in the nests of western gulls (Larus occidentalis) are of frequent (8 to 14 percent of 1200 pairs) and regular occurrence on Santa Barbara Island, California (1, 2). Other field studies (3, 4) show that supernormal clutches occur throughout the colonies of western gulls nesting in the California Channel Islands. A high frequency of supernormal clutches has not been reported for other populations of this species, and the phenomenon is unusual for gulls in general (5-8). Our data suggest that supernormal clutches on Santa Barbara Island are almost always produced by pairs of female western gulls that lay eggs in the same nest and defend a shared territory that has no resident male. Four types of evidence support this conclusion: (i) the sexing of adult gulls captured during incubation, (ii) the intervals between the laying of eggs in normal and supernormal clutches, (iii) the fertility of eggs in normal and supernormal clutches, and (iv) observations of the reproductive behavior of both types of pairs. Data presented here were collected during the breeding seasons of 1972 through 1976.

On normal clutches (one to three eggs), we trapped 10 male and 15 female incubating adult gulls, and one male and 74 females were taken on supernormal clutches (9). On 21 clutches containing one to three eggs, we caught two male-female pairs, eight single males and 11 single females; one additional three-egg clutch was incubated by two females. In contrast, on each of 23 supernormal clutches, we captured two incubating females, and on 27 supernormal clutches, only a single female. In one instance a male-female pair was trapped incubating a clutch of four fertile eggs. The sex of the birds was determined by dissection (1974) or laparotomy (1975 and 1976). The females caught incubating the same clutch apparently form stable pairs. Seven of eight pairs of females laparotomized and banded in 1975 remained paired on the same territories in 1976. Members of homosexual pairs exhibited all courtship and territorial behaviors used by heterosexually mated birds, except that in female-female pairs, courtship-feeding, mounting, and copulation were usually absent. In three female-female pairs, we observed one member of the pair exhibiting behaviors normally

restricted to males, such as mounting and attempted copulation (10). In a few instances females in these pairs regurgitated food in response to repeated head-tossing by the partner in a manner somewhat similar to courtship-feeding by males (11). However, we never observed the females offering large amounts of food as males do in normal courtship-feeding (10). The close interval between the laying of eggs in supernormal clutches (Table 1) (12) indicates that two females were contributing to these clutches. In most larid species, the interval between the laying of the first and second egg and between the second and third egg is similar and, for the larger species, ranges from 2 to 2.25 days (6, 13). These intervals are similar to those found in three-egg clutches in this study. In the supernormal clutches, intervals between the laying of eggs were significantly shorter (t = 7.69, P < .001) (Table 1), and in six instances, two eggs were laid on the same day. The infertility and failure of eggs from supernormal clutches to develop (Table 2) (14) also suggests female-female pairing. If males were usually associated with female-female pairs, one would expect a higher incidence of fertility. The presence of a small percentage of fertile eggs in the nests of female-female pairs can be explained by promiscuous matings. During observations of color-marked birds in 1975, we noted 13 instances in which known male gulls copulated with or attempted to copulate with other gulls not their mates (10). To our knowledge this is the first reported instance of promiscuous matings in gulls in which the females sometimes accepted the males and copulation was successful (15). There are more female-female pairs of western gulls on Santa Barbara Island than are represented by the number of supernormal clutches. We trapped one homosexual pair in 1976 incubating a clutch of three infertile eggs. Of 39 and 19 three-egg clutches examined in 1972 and 1973 respectively, 17.9 and 21.0 percent contained no embryos. During observations in 1972 we were unable to differentiate on the basis of size between members of pairs with three-egg clutches that failed to hatch. Measurements of birds sexed in subsequent years confirmed that this population is sexually dimorphic (10). Had these pairs been heterosexual, differences in size would have been apparent. During hundreds of hours of observation at all phases of the breeding cycle

Table 1. Intervals between the laying of western gull eggs (1973 and 1975) in clutches of different sizes. The number of clutches, number of intervals between consecutive eggs, and the mean number of days between consecutive eggs are indicated.

Table with 8 columns: Clutch size, Clutches (No.), Intervals (No.), Days (X), Same day, Consecutive days, 2 days apart, 3 days apart. It shows data for clutch sizes 3, 4, 5, and 6.

Table 2. Frequency of western gull eggs showing development on Santa Barbara Island. Numerators indicate number of developing eggs, denominators the total examined in each category.

Table with 7 columns: Clutch size, Total number of Clutches, Total number of Eggs, and three columns for Developing eggs (1973, 1974, 1975), plus a Total (%) column. It shows data for clutch sizes 3, 4, 5, and 6.

during five seasons (1972 through 1976), we never observed three gulls defending a territory together or attending the same nest. The presence of two females sharing the same territory cannot be construed as polygamy, regardless of whether or not the eggs produced by those females were fertilized by promiscuous mating with a male. The finding of one male-female pair incubating four fertile eggs does not invalidate the conclusion that the majority of supernormal clutches in the colony are the result of female-female pairing.

Homosexual pairing has not, to our knowledge, been reported for any group of wild birds (16). With the exception of our study it is unknown in gulls, a taxon that has been exposed to widespread and thorough scrutiny. Its existence in western gulls is apparently recent. Before 1968, only two clutches greater than the usual maximum of three eggs were reported for western gulls nesting in the Channel Islands off California and Mexico (17). The first records of substantial percentages of supernormal clutches in this species are from 1968 [11.3 percent of 150 clutches examined, San Nicolas Island (3)] and 1972 [11.0 percent of 63 clutches examined, Santa Barbara Island (1)].

Supernormal clutches have been reported in colonies of ring-billed gulls (*L. delawarensis*) as early as 1942 (7). Vermeer (8) reported that in one supernormal clutch, two eggs were laid on the same day, but no data were presented in any of these studies on either the fertility or the origin of the large clutches in this species.

At present we do not know whether female-female pairing in western gulls is pathological or if it has adaptive value. Promiscuous matings allow some homosexually mated females to produce fertile eggs. Without being paired, they would not be able to incubate these eggs or raise chicks (18). If there were an excess of females in the population (yet to be determined), then homosexual pairing would raise from zero the probability that the excess females would raise offspring.

Although female-female pairs may produce fertile eggs from promiscuous matings, these pairs may still lack other contributions to chick production provided by the male. One difference between pair types is the lack in female-female pairs of net energy input to females by males through courtship-feeding. Eggs laid by the stable homosexual pairs are smaller than those laid by heterosexually paired females (19). Chicks

from small eggs have lower posthatching survival (20). This study may provide a unique opportunity to test the adaptive value of energy provided by the males to the females for egg production.

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References and Notes

1. G. L. Hunt and M. W. Hunt, *Condor* 75, 483 (1973).
2. In 1973, 7.7 percent of 104 clutches; in 1974, 13.8 percent of 65 clutches; in 1975, 10.3 percent of 126 clutches; and in 1976, 8.6 percent of 162 clutches on Santa Barbara Island contained more than three eggs [G. L. Hunt and M. W. Hunt, unpublished field notes].
3. R. W. Schreiber, *Condor* 72, 133 (1970).
4. F. Gress, unpublished field notes; G. Hunt, unpublished field notes.
5. Clutch size in large *Larus* gulls usually ranges between two and three eggs per clutch, and clutches of four eggs are very rare [K. Paludan, *Vidensk. Medd. Dan. Naturhist. Foren. Kobenhavn* 114, 1 (1951); R. A. Fordham, *Notornis* 11, 3 (1964); J. Keith, *J. Appl. Ecol.* 3 (Suppl.), (1966); H. Klomp, *Ardea* 58, 1 (1970); G. L. Hunt and M. W. Hunt, unpublished observations; (1, 6)].
6. K. Vermeer, *Occas. Pap. B. C. Prov. Mus.* 13, 1 (1963).
7. Supernormal clutches of four to six eggs have occurred more frequently in ring-billed gull (*Larus delawarensis*) colonies than in other large *Larus* gulls [J. Moffitt, *Condor* 44, 105 (1942); D. W. Johnston and M. E. Foster, *ibid.* 56, 38 (1954)].
8. K. Vermeer, *Can. Wildl. Serv. Rep.* 12 (1970).
9. Incubating adult gulls were trapped with either walk-in traps placed over their nests [D. K. Weaver and J. A. Kadlec, *Bird-Banding* 41, 28 (1970)] or monofilament snares placed around the edge of the nest, which caught the birds around the feet when the line was pulled.
10. Details of these behavior patterns will be published elsewhere.
11. R. G. B. Brown, *Behaviour* 29, 122 (1967).
12. We determined laying patterns by marking nests with numbered wooden stakes and visiting them daily (1973 and 1975) or every other day (1975) at approximately the same hour in order to record nest contents and individually mark newly laid eggs.
13. Intervals range from 48.7 to 54.8 hours [J. Burger, *Anim. Behav.* 22, 521 (1974)]; R. Drent, *Behav. Suppl.* 7, 1 (1967).
14. In 1973 and 1974, we examined incubated eggs for evidence of development. In 1975, we distinguished fertile from nonfertile eggs on the day they were laid by examining the blastodisc [B. Marquez and K. Ogasawara, *Poult. Sci.* 53, 1607 (1974)].
15. M. MacRoberts [Z. *Tierpsychol.* 32, 62 (1973)] reviewed the literature on "extramarital" courting in gulls and presented detailed information on this behavior for lesser black-backed (*Larus fuscus*) and herring gulls (*Larus argentatus*). In all instances, MacRoberts reported that male gulls attempted to rape females and that the females rejected these advances. No successful copulations were seen. Vermeer (6) reported instances of rape in glaucous-winged gulls (*Larus glaucescens*), which apparently resulted in successful copulations. J. Burger and C. G. Beer [*Behaviour* 55, 301 (1975)] reported rape of incubating female laughing gulls (*Larus atricilla*) by intruding males.
16. Male-male courtship but not pairing has been reported in wild ostriches (*Struthio camelus australis*) [G. Sauer, *Auk* 89, 717 (1972)]. Homosexual pairings of birds in captivity have been reported by N. Collias and L. John [*Auk* 76, 478 (1959)], W. Dilger [Z. *Tierpsychol.* 17, 649 (1960)], and D. Jefferies [*Ibis* 109, 266 (1967)].
17. L. Kiff, unpublished data on museum collections of eggs taken from the Channel Islands of California and Mexico (337 clutches, 1891 to 1969).
18. In 1975, we compared chick survival and growth rates of 37 young produced by 20 normal pairs with 41 foster young given as pipping eggs to 22 pairs that had laid supernormal clutches. Since growth rates and fledging success in the two groups were nearly identical (10), female-female pairs can be considered capable parents under the conditions extant at Santa Barbara Island.
19. G. L. Hunt, M. W. Hunt, R. W. Risebrough, in preparation.
20. J. Parsons, *Nature (London)* 228, 1221 (1970).
21. We thank the personnel of the Channel Islands National Monument for their invaluable help and cooperation. C. Green (1973); S. Anthony, Z. Eppley, P. Ewald, L. Holmgren, D. Schwartz (1975); A. Brand, D. Knapp, G. Kunz, M. Naughton, F. Pierotti, and K. Winnett (1976) have all helped with the fieldwork. Dr. J. Osborne instructed M.W.H. in laparotomy techniques. Financial support was provided by two grants to G.L.H. from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and by the School of Biological Sciences, University of California, Irvine. D. O'Dowd and Drs. D. Anderson, R. Schreiber, R. Risebrough, and K. Vermeer provided helpful comments on various versions of this manuscript.

16 November 1976; revised 4 February 1977

Somatostatin: Analogs with Selected Biological Activities

Abstract. [D -Cys¹⁴]-Somatostatin is the first analog of somatostatin found to be more potent in inhibiting glucagon and growth hormone secretion than it is in inhibiting insulin secretion. [D -Trp⁸]-Somatostatin is eight to ten times more potent than somatostatin in inhibiting insulin, glucagon, and growth hormone secretion. [D -Trp⁸, D -Cys¹⁴]-Somatostatin is more potent than [D -Cys¹⁴]-somatostatin, but retains its relative selectivity in being a more potent inhibitor of the secretion of glucagon and growth hormone than of insulin.

Somatostatin is now recognized as a suppressor of the secretion of various pituitary, pancreatic, and gastrointestinal hormones (1). In addition, somatostatin has been shown to influence an array of neurochemical, neurophysical, pharmacological, and behavioral parameters (1, 2).

The plethora of actions of somatostatin and the demonstrations of its anatomic distribution throughout the central ner-

vous system (3, 4), gastrointestinal tract (4, 5), and pancreas (4, 6, 7) have suggested that somatostatin might play several physiological roles as a local extracellular messenger (1).

Somatostatin when given continuously intravenously (8) or subcutaneously (9) decreases the glucose intolerance of human juvenile diabetes mellitus. This action is at least partially secondary to the lowering of the abnormal elevation of