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COMPARATIVE BEHAVIOR OF MALE-FEMALE AND FEMALE-FEMALE PAIRS AMONG WESTERN GULLS PRIOR TO EGG-LAYING

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ABSTRACT.—The behavior of male-female (M-F) and female-female (F-F) paired Western Gulls (*Larus occidentalis*) before egg laying was examined on Santa Barbara Island, California to test the hypothesis that one female in a F-F pair may assume a male role. In M-F pairs, no behaviors were performed exclusively by either sex, although males Mounted more often, females Head-tossed more often and males acted more aggressively toward intruders. Within F-F pairs, neither partner consistently showed masculine behavior. In a comparison of behavior toward intruders, both members of F-F pairs resembled the female in M-F pairs, and were generally significantly different from males. We therefore reject the hypothesis that female-female pairing is the result of either the adoption of a "male" behavioral role by one or both partners, or an extreme "female" role by one member.

Female-female pairing in natural populations of birds was first documented in the Western Gull (*Larus occidentalis*) on Santa Barbara Island, California (Hunt and Hunt 1977), subsequently in the Ring-billed Gull (*L. delawarensis*) in the Great Lakes and in eastern Washington (Ryder and Somppi 1979, Conover et al. 1979), and in the California Gull (*L. californicus*) in eastern Washington (Conover et al. 1979). In these populations female-female pairing is associated with a frequency of super-normal clutches ranging from 1 to 14%, but this is only a partial index of the frequency of female-female pairs because some female-female pairs produce three-egg clutches. Additionally, abnormally large clutches have been reported for other species (Paludan 1951, Tinbergen 1960, Fordham 1964, Keith 1966, Klomp 1970) in which female-female partnerships might have been involved.

Wingfield et al. (1980a, b) proposed two nonexclusive hypotheses concerning different aspects of the origin of these anomalous, though apparently widespread, female-female associations: (1) Pairs of females may form because there are too few males of breeding age in the population. Hunt et al. (1980) found evidence of such a shortage among Western Gulls on Santa Barbara Island. (2) The process of mate selection by females (Tinbergen 1960, Brown 1967) may require that one of the females adopt male behavior patterns in order for pair formation to occur. We here test the second hypothesis, i.e., that female-female pairing in Western Gulls is facilitated because one of the females behaves like a male, thus effectively deceiving her "mate."

We tested the hypothesis of "masculinization" by comparing the behavior of female-female pairs (F-F) with that of male-female (M-F) pairs during the courtship and territorial period before egg laying. Were the hypothesis correct, at least one member of each F-F pair should conform to the male stereotype. Although the territorial and breeding behavior of several species of gulls has been studied in detail (Moynihan 1955, 1958a, b; Tinbergen 1956, 1959, 1960; Vermeer 1963; Brown 1967; Burger and Beer 1975; Stout 1975), present knowledge of sexual differences in the behavior of large larid species before egg laying (with the exception of Hand [1979] and Pierotti [1981]) is generally qualitative. Therefore, we examined quantitatively the differences in the roles of the partners in both M-F and F-F pairs of Western Gulls during the pre-egg phase of the breeding season.

METHODS

Data were collected on the west side of Santa Barbara Island by five observers from 9 April to 17 May 1976, and from 15 March to 30 May 1977 and in the spring of 1978.

Of approximately 40 pairs observed in 1976

TABLE 1. Duration of observations (minutes) of pairs of Western Gulls.

Pair	Total time	Neither present	Both present	Male or female in "male" role alone	Female or female in "female" role alone
Male–female					
M-F 1	1,414	405	388	154	467
M-F 2	1,109	24	684	222	179
M-F 3	1,068	63	653	103	249
M-F 4	1,595	44	633	197	321
M-F 5	1,151	335	408	114	294
M-F 6	390	124	76	0	190
M-F 7	285	128	95	0	62
M-F 8	734	0	161	449	124
Female-female					
F-F 1	1,439	534	588	168	149
F-F 2	1,244	187	616	230	211
F-F 3	1,585	141	633	735	76
F-F 4	2,395	935	1,023	187	250
F-F 5	1,735	439	745	12	539

and 1977, we selected afterward eight male-female and five female-female pairs for this analysis. In M-F pairs, we either performed a laparotomy on the supposed male or required that the sexes be identifiable by clear differences in size (Hunt et al. 1980). As in other large gulls (Harris and Jones 1969, Ingolfsson 1969), male Western Gulls are significantly larger than females in weight and other mensural characters (Hunt et al. 1980). In four of the eight pairs, sex was judged by estimating size differences; in three, the sex of one individual was determined by laparotomy, and in one pair the male was caught and measured. In all F-F pairs, the sex of both members was determined by laparotomy (Table 1). These operations were usually done after observations were made, although some birds had been examined in a previous year. We also required that at least one member of the pair be individually identifiable by either color-bands or dye-markings, and that the pair's entire territory be visible to the observer throughout the observation period. Birds observed for less than 100 min for a given comparison were not used in that comparison (observation periods in Table 1).

We have few data on the history of these pairs. The behavior of newly formed pairs and those that re-formed after a winter's absence may differ both quantitatively and qualitatively. Detailed analysis was possible for only 20 days before the onset of oviposition in 1976. Because we wished to combine data from both years, we limited our analysis to this period.

All pairs were watched from blinds at least once every five days until the first egg was laid. Observations were made in the morning (05:30–11:00) and/or early evening (16:30–dusk), periods of maximal activity and colony attendance for this species (G. L. Hunt, Jr., and K. Winnett, unpubl.). The following behaviors were recorded for each individual in one to several pairs: 1) presence on territory, 2) Long Call, 3) Mew Call, 4) Choke, 5) Head-tossing (with or without simultaneous vocalization), 6) Face Away, 7) Courtship-feeding (including pronounced neck bulges and unsuccessful regurgitation attempts), 8) Mount, 9) Copulate, 10) nesting activity (including gathering nest material, nest-building and sitting on an empty nest), 11) Aggressive Upright, 12) Supplant (movement toward another bird resulting in its displacement), 13) Grass-pulling, and 14) fight (for descriptions, see Tinbergen 1959, 1960).

Because of the difficulty in determining when certain displays ended (e.g., Choking and Head-tossing), observers simply noted whether or not a behavior was performed within each minute. This procedure enabled us to monitor more birds and to ensure consistency among observers although it caused some statistical disadvantages (Altmann 1974).

For each display recorded, the observer noted whether it was directed toward the mate or toward another bird (either a neighbor or intruder). The direction was difficult to tell in many bouts of Choking that involved both members of a pair, so all Choking was assumed to be an exchange between mates unless it was clearly directed elsewhere. Also, most mobile Aggressive Upright displays had no apparent recipient, so they were assumed to be directed toward birds outside the pair.

To distinguish between male and female behavior patterns, we used the sign test (Siegel 1956) to compare the frequency of occurrence of behavior types within M-F pairs. Two types of behaviors were compared: 1) behavior directed toward the mate related to courtship and mating, and 2) behavior directed toward territorial intruders a) when the mate was present and b) when the mate was absent. The behavior profiles of the eight M-F pairs were used in these comparisons.

To compare behaviors of members of F-F pairs, we needed a method for identifying females who might have adopted a "male" role before we could compare differences either within these pairs or between members of these pairs and members of M-F pairs. We categorized F-F paired birds into two groups on the basis of three courtship behaviors: Head-tossing (performed mostly by females in M-F pairs) and Courtship-feeding and Mounting (performed mostly by males). Whichever female

TABLE 2. Classification of roles for female-female pairs of Western Gulls during courtship.

Pair	Number of occurrences of behavior: Courtship feeding		Mounting		Head-tossing		Individual classified as in "male" role	Strength of differentiation of roles*
	Bird A	Bird B	Bird A	Bird B	Bird A	Bird B		
F-F 1	2	3	0	0	25	25	B	Weak
F-F 2	6	5	8	0	51	53	A	Moderate
F-F 3	3	1	0	0	65	67	A	Moderate
F-F 4	1	1	6	0	46	41	A	Moderately strong
F-F 5	1	1	0	8	44	28	B	Moderately strong

* Subjective evaluation of our certainty in assigning roles.

exhibited more male-like behavior than her mate for at least two of these behaviors was classified as the bird in the "male" role. Using the groupings of F-F pairs thus derived, we compared the behavior toward intruders of these two groups of females, with and without their mates present, within pairs, and with both members of M-F pairs. Since the data consist only of normalized frequencies (minutes with acts/minutes of observation of behaviors for each member of both M-F and F-F pairs) we used the sign test (Siegel 1956) to test the null hypothesis that half of the observed frequency differences would be positive and half negative.

RESULTS

BEHAVIOR OF MALE-FEMALE PAIRS

We were unable to separate males from females on the basis of overall behavior patterns when all courtship and mating behaviors were examined together. However, males Mounted more than females ($P < 0.01$), and females Head-tossed more than males ($P < 0.01$). Moynihan (1958b) and Tinbergen (1960) also found Head-tossing more commonly performed by females. Additionally, in five of the eight pairs, males Courtship-fed more than females, while in the other three pairs no Courtship-feeding was recorded. We saw females Mount males and once saw a female Courtship-feed her mate; males frequently engaged in Head-tossing.

We found that males were more active toward intruders than females when all behaviors were examined together, whether the males were alone on territory ($n = 24$, $\bar{x} = 5$, $P < 0.01$) or were with their mate ($n = 22$, $\bar{x} = 5$, $P < 0.01$). In these conflicts, however, only one behavior when examined by itself, Supplanting ($P < 0.05$), differed between the sexes, and no behaviors were performed exclusively by one sex. Individual variation in behavior was sufficiently great that we could not judge sex solely by the rates at which members of a pair performed these agonistic behaviors unless the behaviors of the mates were known. Females were more active toward intruders when their mate was present than in his absence ($n = 26$, $\bar{x} = 6$, $P \leq 0.01$). The behavior of males toward intruders did not differ according to the presence or absence of their mates.

BEHAVIOR OF FEMALE-FEMALE PAIRS

The differences in the use of Head-tossing, Mounting, and Courtship-feeding by males and females in M-F pairs provided criteria by which we separated members of F-F pairs into two categories (Table 2). Classification of the birds in terms of courtship behavior was fairly clear for pairs F-F2, F-F4, and F-F5 in which considerable Mounting behavior was observed, but less so for the birds in F-F3 and especially F-F1. These classifications allowed us to test the hypothesis that females who were assumed to have a relatively greater "male" role behaved differently from their partners toward intruders. We predicted that females who Mounted more, did more Courtship-feeding, and less Head-tossing would more closely approximate male levels of activity, while their female partners would be more like females within M-F pairs.

The two females of F-F pairs were indistinguishable in their behavior toward intruders, whether or not their partners were present. This contrasted with the behavior of M-F pairs. Females that were classified as having a greater "male" role on the basis of courtship behavior did not show higher levels of agonistic activity than their partners. Neither class of females changed its behavior toward intruders with respect to the presence or absence of its mate.

Randomly, we matched females from the five F-F pairs with males and females from the eight M-F pairs (Table 3). We found that members of F-F pairs did not differ significantly from females in M-F pairs in the frequency of agonistic behaviors directed toward intruders. In three comparisons (Table 3) females in F-

TABLE 3. Comparison of females from female-female pairs with males and females from male-female pairs in their reaction toward intruders. Summary of sign tests for the similarity between randomly matched birds of different classes. Null hypothesis = no significant difference in the frequency of behaviors toward intruders.

	Male-female pairs					
	Males			Females		
Female-female pairs	*n*[b]	×	*P*	*n*	×	*P*
Females in "male" role with mate (5)[a]	28	8	≤0.05	25	12	n.s.
Females in "male" role alone (4)	20	5	≤0.05	14	6	n.s.
Females in "female" role with mate (5)	28	7	≤0.05	24	12	n.s.
Females in "female" role alone (4)	16	7	n.s.	13	3	≤0.10

[a] Number of pairs available for comparison.

[b] The number of behavior comparisons with a sign difference (pairs × behaviors).

F pairs differed significantly from males in M-F pairs.

We also compared the two categories of birds in F-F pairs with members of M-F pairs for the frequency with which three courtship behaviors (Courtship-feeding, Mounting and Head-tossing) were given (Table 4). Both categories of females from F-F pairs could not be distinguished from females in M-F pairs when paired comparisons between randomly matched birds were made. In contrast, both classes of females in the F-F pairs differed from males in similar comparisons. Thus, for these courtship behaviors neither class of partner in F-F pairs appeared to behave like a male.

In M-F pairs, males appeared to spend less time on their territories than females. Including other pairs not in the behavioral analysis, females spent more time on territory in days 1–10 than in days 11–20 before egg laying (Wilcoxon matched pairs sign test $T = 0$, $n = 11$, $P < 0.002$). In F-F pairs, birds in the "male" role category did not tend to spend less time on the territory as onset of egg laying approached. With the small sample of time on the territory for members of F-F pairs, we were unable to tell whether their patterns of territorial attendance were more similar to those of males or females in M-F pairs.

Qualitative differences in the courtship behaviors of males and females were real, but hard to define. The vigor of Head-tossing by females and the mode of performance of Mounting and Courtship-feeding by males allowed us to distinguish between the sexes. Mounting by females was frequently disoriented, with birds standing sideways or even head to tail, and often was incomplete. Courtship-feeding by females differed from that of males in that females usually reingested the food immediately after regurgitating and rarely allowed their mates to eat. On the other hand, some "male" courtship behaviors exhibited by females in F-F pairs were qualitatively similar to those of males. In one instance, a female (not included in the tabulated statistics) Mounted, attempted Copulation with her mate, and gave the Copulation Call.

TABLE 4. Comparison of females from female-female pairs with males and females from male-female pairs in their use of courtship behaviors. Summary of sign tests for the similarity between randomly matched birds of different classes. Null hypothesis = no significant difference in the frequency of the courtship behaviors: Courtship-feeding, Mounting and Head-tossing.

	Male-female pairs					
	Males			Females		
Female-female pairs	*n*	×	*P*	*n*	×	*P*
"Male" role (5)	15	2	≤0.01	14	3	≤0.10
"Female" role (5)	15	2	≤0.01	11	3	≤0.25

DISCUSSION

Our results do not support the hypothesis that F-F pairs have formed because one or both members of the pair behave like males. Males and females in M-F pairs differ consistently not only in three courtship behaviors, but also significantly in the frequency with which they react to intruders.

Within F-F pairs we could identify individuals that showed somewhat more "male" behavior during courtship than their "mates" (Table 3). Nevertheless, several lines of evidence indicate that both members of F-F pairs are more similar to the females than the males of M-F pairs (Tables 3 and 4). Males showed consistent patterns of courtship, territory attendance and agonistic behavior, even though in many cases they differed only in small degree from females. In contrast, females in F-F pairs that showed more of the typically male courtship behavior did not consistently behave like males in other ways (less aggressive toward intruders, 3/5 spent more time on territory). The consistency in the behavior of males argues for our method of assigning categories for the females in F-F pairs, while the lack of consistency in these females argues against the hypothesis that one member of each

F-F pair behaved like a male. Our sample sizes are small, and therefore these results should be considered preliminary. They agree with the finding of no evidence for endocrine "masculinization" of either female in F-F pairs (Wingfield et al. 1980a, b, 1981).

Our study did not directly examine the process of pair formation but focused on mate interactions and territorial behaviors after the formation of a pair bond. We do not know what features females seek when choosing mates. Therefore, it is still possible that females in F-F pairs resemble males during the initial pairing, a process that we have not had the opportunity to observe. The lack of strikingly different male and female behaviors and the existence of size overlap between the sexes may facilitate F-F pairing in the presence of a skewed sex ratio (Hunt et al. 1980). What is less clear is how these gulls normally identify the sex of a prospective mate, given the overlapping continuous dimorphism (Burley 1981) of Western Gulls.

One hypothesis (Hunt 1980) is that, in sexually monomorphic species, there is no mechanism whereby sex, per se, is recognized. Rather, potential partners may be judged on a variety of characters which vary in an essentially continuous, quantitative way between males and females. In these cases, behavioral interactions would most often yield male-female matings, but there would be no absolute prevention of homosexual pairings. When the "best" available individuals were of the same sex, homosexual pairings could occur. This hypothesis is compatible with our observations of Western Gulls and Burley's (1981) observation of the lack of sexual recognition in pigeons, but it remains to be critically tested.

Male and female behaviors overlap more than expected on the basis of the descriptions of Tinbergen (1960) and Brown (1967); moreover the behaviors exhibited by females changed depending on social context or environmental factors (Pierotti 1981). Females in F-F pairs may be more like males in their response toward intruders when these females are alone on territory (Table 3). Pierotti (1981) showed that female Western Gulls behave less aggressively toward intruders than do males, although he did not specify whether his birds were alone on territory. We found that females in M-F pairs, when alone, occasionally responded to intruders more actively than did their mates when the latter were alone on territory (two of six cases). Females were consistently less active in the presence of their male partners (seven out of seven cases); overall, females responded less actively toward intruders when alone on territory than when their male partners were present. This differs from Pierotti's (1981) result on Southeast Farallon Island, where 70% of female aggressive acts occurred while their male partners were absent. Perhaps the less aggressive behavior ascribed to female gulls is a modification in order to coexist with aggressive male partners. Clearly, members of F-F pairs are capable of a greater range of courtship behaviors and possibly a higher frequency of agonistic behavior than is commonly expressed by females in M-F pairs (Table 3, female in female role alone). Our observations of females Mounting and Courtship-feeding are contrary to the reports of Moynihan (1955) and Tinbergen (1960) that these behaviors are performed exclusively by males.

Mounting of males by females has been recorded for several avian species other than gulls and female-female mating has been recorded in at least one other group. Williams (1942) and Kortlandt (in Williams 1942) described how female Brandt's Cormorants (*Phalacrocorax penicillatus*) may perform most if not all displays given by males and that either sex may Mount. In the communally nesting subspecies of the Purple Swamphen (*Porphyrio porphyrio melanotus*), Craig (1980) found not only reverse Copulations, but also female-female and male-male Copulations, and female-female Courtship-feedings. Mounting of males by females has also been recorded for several passerines (Thompson and Lanyon 1979, and references cited therein). These observations reinforce our idea that female birds may, under some circumstances, take a more assertive role in mating than is usually assumed and that stereotypes of male and female behavior may obscure the complexity and subtlety of interactions between the sexes.

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