

**A MATHEMATICAL MODEL TO ESTIMATE THE
FREQUENCY OF FEMALE-FEMALE OR OTHER
MULTI-FEMALE ASSOCIATIONS
IN A POPULATION**

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Female-female pairs have been reported in several gull species (Hunt and Hunt 1977, Conover et al. 1979, Conover 1984a, Ryder and Somppi 1979, Shugart 1981), and in the Caspian Tern (*Sterna caspia*; Conover 1983). In all of these species, female-female pairings were detected because they often produce unusually large or supernormal clutches (Conover 1984b). These female-female pairings result when two females associate at the beginning of the breeding season (Conover 1984c), defend a single territory, lay eggs in the same nest, and share parental responsibilities (Hunt and Hunt 1977). Polygyny also occurs in Ring-billed Gulls (*Larus delawarensis*; Conover et al. 1979, Lagrenade and Mousseau 1983, Conover 1984a) and Herring Gulls (*L. argentatus*; Shugart 1981). Hereafter, such breeding associations where two or more females lay eggs in the same nest and share parental responsibilities (polygyny or female-female pairs) will be called a multi-female association (MFA).

The reason why females form an MFA is unclear because the reproductive success of females paired monogamously with males usually is higher than those in MFAs (Hunt and Hunt 1977, Kovacs and Ryder 1983). One hypothesis is that MFAs occur when some females are unable to obtain male mates due to a shortage of breeding males (Hunt and Hunt 1977). This hypothesis was supported by the finding that females outnumbered males at a Western Gull (*L. occidentalis*) colony where female-female pairings occurred (Hunt et al. 1980) and by the demonstration that supernormal clutch frequencies (and presumably MFAs) increased in Ring-billed and California gull (*L. californicus*) colonies where the breeding adult sex ratio was experimentally skewed by removing males (Conover and Hunt 1984a). Based on museum collections, females also appeared to outnumber males in some species and populations where female-female pairings occurred (Conover and Hunt 1984b).

A major difficulty in understanding the significance of MFAs in colonial waterbirds is the lack of population data on MFAs which, in turn, stems from the difficulty of identifying and counting MFAs. Since sexual dimorphism is so slight in gulls (e.g., Ryder 1978), most individuals cannot be reliably sexed unless the birds are caught and measured or their gonads inspected. Thus one can feasibly sample only a small number of gulls, making estimates of MFA frequencies unreliable. A faster and simpler way of estimating the frequency of MFAs in a population is by counting the number of supernormal clutches in a colony and assuming that the MFA frequency is equivalent to the frequency of

supernormal clutches. There are two problems with this assumption: (1) some supernormal clutches may not be attended by MFAs, particularly 4-egg clutches (Conover 1984a) and (2) some MFAs attend normal-sized clutches (Hunt and Hunt 1977, Ryder and Somppi 1979, Conover et al. 1979, Conover 1984a). The latter factor makes estimating MFA frequencies particularly difficult because although only a small percentage of normal-sized clutches may be attended by MFAs, they may still have a major effect on MFA frequencies.

In this paper, we propose an alternative method of estimating the frequency of MFAs in a population, one that uses a mathematical model. The model requires the investigator to determine the number of 4-, 5-, and 6-egg clutches which are attended by MFAs, an operation that requires the sexing of a much smaller number of gulls (because most of these are attended by MFAs). The model then uses these data to determine the frequency of MFAs attending normal-sized clutches. In this paper, we present this mathematical model, discuss its assumptions, and use it to determine the frequency of MFAs in the Pacific Northwest Ring-billed and California gull populations, using data from Conover (1984a).

THE MATHEMATICAL MODEL

We estimated the total frequency of MFAs in gull colonies based on 3 assumptions. We assumed (1) that each MFA consisted of two females, both of which lay at least one egg, (2) that no individual female in an MFA lays more than 3 eggs, and (3) that females pair randomly with respect to each female's egg-laying potential. Given these assumptions, MFAs had to produce a 2- to 6-egg clutch. Because the number of 4-, 5-, and 6-egg clutches attended by MFAs could be easily determined by observation, the problem for the model was to estimate the number of 2- and 3-egg clutches attended by MFAs. To compute the total frequency of MFAs in a colony we let:

- a = no. of 2-egg clutches resulting from MFAs (an unknown value);
- b = no. of 3-egg clutches resulting from MFAs (an unknown value);
- C = no. of 4-egg clutches resulting from MFAs (determined from data);
- D = no. of 5-egg clutches resulting from MFAs (determined from data);
- E = no. of 6-egg clutches resulting from MFAs (determined from data);

and we let

- x = probability of an MFA female contributing 1 egg to the nest;
- y = probability of an MFA female contributing 2 eggs to the nest;
- and
- z = probability of an MFA female contributing 3 eggs to the nest.

We have distinguished between unknown values by lower case letters and values determined observationally by upper case letters. According

to our assumptions, $x + y + z = 1$ and $a + b + C + D + E =$ the total number of clutches laid by MFAs.

We assume that females pair randomly to form MFAs and thus we equate the probability of different-sized clutches resulting from a pairing of females (each of which may contribute 1, 2, or 3 eggs to a nest) to the relative frequency of 2-, 3-, 4-, 5-, and 6-egg clutches. Doing this, we obtain the following 5 equations containing the 5 unknown values: x , y , z , a , and b :

$$\begin{aligned}
 x^2 &= \frac{a}{a + b + C + D + E} \\
 2xy &= \frac{b}{a + b + C + D + E} \\
 2xz + y^2 &= \frac{C}{a + b + C + D + E} \\
 2yz &= \frac{D}{a + b + C + D + E} \\
 z^2 &= \frac{E}{a + b + C + D + E}
 \end{aligned}$$

From these equations we find algebraically that

$$\sqrt{a} = \frac{1}{2\sqrt{E}} \left(C - \frac{D^2}{4E} \right) \quad b = \frac{D}{2E} \left(C - \frac{D^2}{4E} \right)$$

To determine the MFA frequency for the Ring-billed Gull population in Washington and Oregon we used the model on the following data from Conover (1984a):

Clutch size	1	2	3	4	5	6
No. nests	1213	3873	13,526	618	123	33
No. due to MFAs	0	a	b	C = 185	D = 123	E = 33

We used these data to solve for a and b (the number of 2- and 3-egg clutches attended by MFAs) and found that $a = 38$ and $b = 131$ so that the total number of clutches resulting from MFAs is 510 or 2.6% of all nests. This yields $x = 0.271$, $y = 0.474$, and $z = 0.254$.

We also used the following data from Conover (1984a) to calculate the values a and b for the Washington and Oregon California Gull population:

Clutch size	1	2	3	4	5	6
No. nests	473	1860	2964	53	4	1
No. due to MFAs	0	a	b	C = 15	D = 4	E = 1

We found $a = 30$ and $b = 22$ so that the total number of clutches resulting from MFAs is 72 or 1.3% of all nests. This yields $x = 0.645$, $y = 0.237$, and $z = 0.118$.

DISCUSSION

Our model predicts the number of MFAs which were attending nests in a colony or population at the time the data were collected. The obtained values do not include any MFAs which had already lost their entire clutch and ceased incubating at the time of the survey or any MFAs which had not yet started to lay eggs.

The 3 assumptions of the mathematical model are that (1) two females lay eggs in each MFA nest, (2) each female in an MFA lays a 1-, 2-, or 3-egg clutch, and (3) females in MFAs pair with each other without regard to the other's egg-laying ability. These assumptions, however, may not always be entirely valid. Rarely, 3 or more females may lay eggs in the nest. Nonetheless, by assuming that only two females lay eggs in each MFA, our estimates of the frequency of MFAs are slightly conservative compared to what they would be if some of these clutches actually contained eggs from 3 or more females.

Likewise, our model does not count MFAs in which only one female has contributed eggs to the nest at the time of the study. The major concern here is that eggs laid by one female in the nest may entirely inhibit the other female's egg laying. Paludan (1952) showed that by putting eggs in Herring Gulls' nests before the gulls started laying, he could reduce the number of eggs eventually laid from 3 to 2. It also appeared that in one or two cases, he might have entirely suppressed egg laying. If the latter also occurred at MFA nests, these nests would be excluded from our analysis, making our estimates conservative. Another consideration is egg loss from MFA nests. Egg loss would have no effect on our model unless a female lost every egg she laid in an MFA nest. In that case, the nest would be excluded from our analysis since our model counts only nests where two females contributed at least one egg to the nest at the time of the survey. Hence high egg loss would further make our estimates conservative.

Our second assumption that females in MFAs do not individually lay more than 3 eggs may not always be true. Between 1-2% of the Ring-billed and California gull nests in the Pacific Northwest colonies contained 4 eggs, but MFAs account for approximately 30% of these nests (Conover 1984a). In the Great Lakes, Fetterolf and Blokpoel (1984) have also shown that many 4-egg clutches in Ring-billed Gulls result from nest parasitism. Hence, most 4-egg clutches were probably laid by more than one female. Because females in MFAs generally lay fewer eggs than monogamous females, the likelihood of an MFA female laying a 4-egg clutch is even smaller. It probably happens, but we argue that it happens infrequently enough that the error produced in our model by ignoring it is small. Nevertheless, this error, if it exists, would also make the predictions of our model slightly conservative.

Our third assumption is that the females in MFAs pair randomly with respect to the number of eggs each female will lay. We do not know the criteria used by an MFA female in selecting a mate and whether these correlate with egg-producing ability. If MFA females with high egg-producing potential tend to pair together, and similarly for those with low potential, our model will again underestimate the total frequency of MFAs in the population. Therefore, violations of any of our assumptions will mean that predicted frequencies of MFAs in a population will be conservative.

Nest parasitism should have no effect on our model or its predictions, but may influence how the necessary data for the model are collected. Our model requires that the number of MFAs attending 4-, 5-, and 6-egg clutches be known. The easiest way to do this is just to count the number of supernormal clutches in a colony and assume that all are caused by MFAs. This assumption, however, may not be accurate due, in part, to nest parasitism. Because of this, it is necessary to determine what proportion of these nests are attended by MFAs. For instance, Conover (1984a) showed that while all examined 5–6-egg clutches were attended by MFAs, most 4-egg clutches in Ring-billed and California gulls were not. Apparently nest parasites in these colonies usually do not lay more than one egg in the same nest, creating few 5–6 egg clutches. This may or may not be true in other species.

The advantage of our model is that it saves the investigator from having to make a direct determination of the MFA frequencies among normal-sized clutches. Such a task is time-consuming for it would require sexing all adults at hundreds of nests, a difficult feat in sexually monomorphic species. For instance, using data from Conover (1984a), our model estimated that 2.6% of the breeding population of Ring-billed Gulls and 1.3% of California Gulls consisted of MFAs in the Pacific Northwest. Thirty-three percent of the MFAs in Ring-billed Gulls were estimated to have normal-sized clutches, as were 72% of the MFAs in California Gulls. Hence the error which would have been produced by ignoring these birds and assuming that all MFAs produce supernormal clutches would have been large. Yet at the same time, our results indicate that these MFAs accounted for only about 1% of all normal-sized clutches so that it would have been very difficult to determine their number directly.

SUMMARY

The frequency of female-female pairings and polygynous associations (known as multi-female associations or MFAs) in colonial waterbirds is usually estimated by assuming that their frequency is equivalent to the frequency of supernormal clutches in a population. Such estimates are often inaccurate, because some MFAs attend normal-sized clutches. However, a direct determination of the MFA frequencies among normal-sized clutches is time-consuming; such would require sexing all adults at hundreds of nests, a difficult task in sexually monomorphic species.

As an alternative, we devised a probabilistic mathematical model that calculates the total frequency of MFAs in a population, providing that the number attending 4-, 5-, and 6-egg clutches is known. Using data from Conover (1984a), this model predicted that 2.6% of all Ring-billed Gull nests and 1.3% of all California Gull nests in the Pacific Northwest were attended by MFAs. In contrast a count of 5- and 6-egg clutches would have estimated MFA frequencies at only 1.56% in Ring-billed Gulls and 0.30% in California Gulls.

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