

## Comparative biology and behavior of monogamous pairs and one male-two female trios of Herring Gulls

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**Summary.** In northern Great Lakes Herring Gulls one male-one female pairs are the predominate breeding association. We found that 0.6% to 1.0% of the nests from 1978 to 1981 were attended by one male-two female trios in which both females laid eggs. Individually marked birds in trios remated in successive years in 77% of the instances which was not significantly different from pair fidelity.

Trios were comprised of a male and a primary female, which may have been a pair in previous years, and a secondary female bonded to the male.

We found that although a trio male might potentially benefit from breeding with 2 females because of a larger clutch-size, this does not increase his annual reproductive success. Reproductive success of secondary females was much lower than primary and pair females' success. Reasons for the poor reproductive output of secondary females relative to pair and primary females were significantly lower egg fertility and lower hatching success of fertile eggs. Lower hatching success of fertile eggs in trios' nests largely results from termination of incubation of secondary females' eggs when the earlier laid eggs of the primary females' hatched. In addition, eggs may be shifted between cups of a double-nest. Fertile eggs of trio females may not hatch because both cups are not incubated continuously.

The hypothesis that a secondary female joined a mated male because the increase in annual reproductive success offsets the costs was rejected. It is also doubtful whether a female lives long enough to produce sufficient young to make secondary status adaptive. Secondary status may familiarize the secondary female with the male when there are too few males available.

### Introduction

The common mating relationship in long-lived seabirds is a one male-one female pair in which members of each sex share the cost of care of their offspring by alternating feeding at distant food sources and incubating, brooding, and defending the territory and offspring. Although polygamous associations have been reported in seabird species (e.g. *Larus canus*, Nethersole-Thompson and Nethersole-Thompson 1942; *Catharacta skua lonnbergi*, Bonner 1964, Young 1978; *Sterna sandvicensis*, Smith 1975; *Larus delawarensis*, Conover et al. 1979; *Larus argentatus*, Shugart 1980), the significance of these associations is unknown.

There are several hypotheses which could explain the occurrence of trios in the Herring Gull. Because of an operational or actual skew in the sex ratio in the population 1) an unmated female may be joining an already mated male because she is able to reproduce as successfully as a secondary mate than as a primary female or pair female (Orrians 1969; Emlen and Oring 1977), or 2) she increases her survivorship even though yearly reproductive success declines (Elliot 1975), or 3) males may be mating with female pairs which are present in the study area (Shugart 1980).

In this paper we examine these hypotheses by a comparison of individually marked and sexed birds in one male-two female trios in which the male associates with 2 females and both females lay eggs (hereafter referred to as trios) and one male-one female pairs (hereafter referred to as pairs) in Great Lakes Herring Gulls.

### Materials and methods

The frequency of trios and pairs was monitored by censuses of 7, 6, 7, and 5 colonies respectively, in northeastern Lake

Michigan in 1978 through 1981 during the last 2 weeks of incubation.

Trios usually build double-nests which consist of 2 cups, 30–60 cm center to center, which are joined with nest material. We included only double-nests in which each cup contained at least 1 egg, or in the few cases we saw the secondary female lay in the same nest cup as the primary female. The number of eggs in single and double-nests were recorded during censuses in 1978 (see Shugart 1980), 1979, 1980, and 1981 to sample clutch-size. To determine if the number of eggs found in double-nests was a reliable indicator of the number laid, we marked eggs in a sample of double-nests prior to censusing. From these data we calculated egg survival rates. Additional data concerning egg survival rates were obtained from trios which we observed from blinds.

The adults in the breeding groups from which comparative reproductive and behavioral data were collected were sexed through unilateral laparotomy (Bailey 1951) or measurements (Shugart 1977) and banded with US Fish and Wildlife Service bands and color-bands.

It is difficult to obtain data which permit comparison of fitness (i.e. the number of offspring which live to reproductive age and survivorship of adults, Fisher 1958). We measured variables that we feel are good indicators of fitness and used these variables for comparison of trios and pairs. Reproductive variables used included clutch-size, egg fertility, hatching success, and chick survival to flying. For uniformity in all years, clutch-size was the number of eggs present in nests prior to hatching.

A large sample of egg fertility of trios (see criteria below) was obtained by marking eggs found in double-nests during censuses and visiting the nests repeatedly to determine the fates of eggs.

Fertile eggs included those that pipped or hatched as well as eggs which contained embryos. The only eggs opened and examined for presence of embryos were those that did not float as predicted if normal development was progressing (see Schreiber 1970). Eggs that contained yolks, but no embryonic development after at least 2 weeks of incubation were classified as infertile. Comparison of eggshell color, using Smithe (1976) as a standard, was used in 1979 to determine the amount of within clutch variation of pairs in an attempt to distinguish clutches of trio females in double-nests.

Chick survival was determined by observation from blinds of individually marked young. Young were banded before they could run, or remotely marked with paint from the blind. We used above-ground tunnels (Shugart et al. 1981) to enter and exit observation blinds to eliminate bias from chick mortality that would have been induced by our disturbance.

Chick survivorship could be increased by the presence of 3 birds in a trio if the 3 birds provided better protection from inclement weather or predation, or if 3 birds provided more food than the 2 birds in a pair. We compared protection using the amount of time chicks were left alone on the territory in trios and pairs by using 15 min instantaneous scan sampling.

We used total number of feedings per chick as an indirect measure of feeding. We used this indirect measure to avoid chick mortality that could result from disturbing the colony in an effort to obtain chick weights and measurements. These data are interpreted cautiously because frequency of feeding does not necessarily indicate the amount of food delivered.

To determine if individuals in trios reduced input per reproductive effort (hypothesis 2), thereby possibly increasing adult survivorship relative to pairs, we sampled an individual's contribution to the group using 3 behavioral variables; 1) relative frequency of aggression toward non-group members. We used relative frequencies instead of absolute rates because intrusion rates and therefore aggression, between territories can vary

(Ewald et al. 1980), 2) number of chick feedings standardized by the number of chicks, and 3) territory guarding which was the percent of observation time an individual spent on the territory.

Behavioral data are based on 5,654 group (trio and pair) hours of observation between late incubation to fledging in 1977 to 1980, and 2 weeks prior to laying until fledging in 1981. The 33 groups were observed an average of  $171.3 \pm 100.8$  h each.

Aggressive encounters between trio members were also quantified. In trios in which intragroup aggression occurred the dominant female in female-female interactions, which was also the female most closely associated with the male, was designated the primary female.

Means  $\pm$  one standard deviation are indicated.

## Results

### *Frequency of trios*

At 7, 6, 7, and 5 colonies in northeastern Lake Michigan in 1978 through 1981 respectively, 0.7% (28/4116) (from Shugart 1980), 1% (37/3784), 0.6% (24/3952), and 0.8% (43/5045) of the total nests were double-nests. The proportion of the nests which were attended by trios between years was not different ( $\chi^2 = 4.16$ ,  $P > 0.1$ ).

To estimate the fidelity of trios relative to pairs, we determined the probability that a pair or trio would remain together by finding the number of intervals between years that members of trios and pairs still associated. In 13 between-year intervals for 9 marked trios there was a 77% (10/13) probability that a trio remained together. In 14 between-year intervals for 12 marked pairs there was a 100% (14/14) probability that a pair remained together. This indicates that once a trio forms, the 3 birds will associate in successive years. The probability that trios will remain together is not significantly lower than fidelity of pairs ( $G = 2.4$ , Yate's correction for continuity,  $P > 0.1$ ).

In 2 instances we know the circumstances when trios formed. In one, a female that was in a trio for 1 year which broke up, associated with a previously marked adjacent pair for 3 successive years. In the other, a female joined a marked pair observed in the previous year.

### *Double-nest clutch size*

In 132 double-nests found between 1977–1981; 48% (63/132) had 3 eggs in 1 cup and 1 egg in the other cup; 24% (32/132) had 3 eggs-2 eggs; 9% (12/132) were 4 eggs-1 egg; and 8% (10/132) had 3 eggs-3 eggs. Nine other combinations occurred less than 5% of the time.

In 13 double-nests, we marked 63 eggs and found that no eggs had disappeared when we cen-

sused  $9.2 \pm 7.2$  days later. Therefore, the number of eggs present in double-nests at our census, done when the majority of the colony was in the last 2 weeks of incubation (see Shugart 1980), provides a reliable indicator of the number of eggs that had been laid.

### Fertility

Of 53 double-nests which were investigated for fertility; 63% (157/250) of the eggs were fertile; 25% (62/250) of the eggs were infertile; and 12% (31/250) of the eggs could not be classified as fertile or infertile because they were rotten. In 21% (11/53) of the double-nests all eggs were fertile. In 41 pairs' nests 99.2% (120/121) of the eggs were fertile and 0.8% (1/121) of the eggs were infertile.

Control studies with pairs proved eggshell color was an unreliable indicator to distinguish females' clutches in trios because within clutch variation was great. In 33 pairs' 3-egg clutches, 58% (19/33) nests had eggs that were different (also see Schreiber 1970; Chamberlin 1975). Therefore, we only determined which female laid which egg in 6 trios' nests by observation.

### Reproductive comparison of pairs and trios

Reproductive data in addition to clutch-size and fertility were collected from a subsample of the 132 trios and 41 pairs most of which were observed in consecutive years.

Trios in the subsample started out with a mean clutch size of  $4.8 \pm 0.8$  ( $N=18$  trios) as compared to  $2.9 \pm 0.3$  eggs per pair ( $N=25$  pairs). This significant ( $U=450$ ,  $P<0.001$ ) disparity between groups in reproductive potential for the males does not persist through fledging. In fact both types of breeding groups rear an equivalent number of offspring ( $N=14$  trios, mean =  $2.1 \pm 0.9$ ;  $N=23$  pairs, mean =  $2.1 \pm 0.7$ ). Therefore, males raise an equivalent number of young whether they associate with 1 or 2 females.

Comparison of female success is not as straightforward because it depends upon egg ownership. Of 6 trios in which we knew egg ownership, the primary female laid  $3.0 \pm 0.0$  eggs which was a significantly greater clutch-size ( $U=30$ ,  $P<0.05$ ) than the secondary females' clutch of  $2.0 \pm 0.9$  eggs. Primary females in these 6 trios raised  $2.2 \pm 1.3$  offspring to fledging, whereas secondary females only produced  $0.33 \pm 0.5$  offspring. The significantly lower average annual production by secondary females ( $U=31$ ,  $P=0.05$ ) depends not only on smaller secondary females' clutches, but

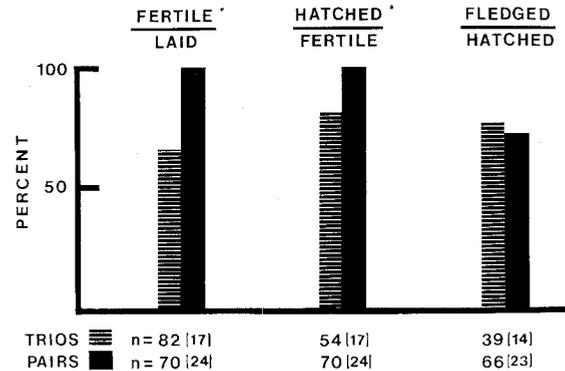


Fig. 1. Comparison of trio and pair reproductive data. Denominators used in calculation of percents are indicated below each bar and the number of groups are in parentheses. Values based on the numerical data are: eggs fertile and not fertile,  $\chi^2=27.07$ ,  $P<0.01$ ; eggs hatched and not hatched,  $\chi^2=11.71$ ,  $P<0.01$ ; chicks fledged and not fledged,  $\chi^2=0.22$ ,  $P>0.5$

also reflects lower success in raising offspring from eggs. Primary females raised offspring to fledging from 72% (13/18) of their eggs, whereas secondary females fledged only 17% (2/12) of secondary females' eggs ( $G=7.15$ , Yates correction for continuity,  $P<0.01$ ). The lower success in producing offspring by trios, compared with pairs, and by secondary females, compared with primary females, results from differences in egg fertility and hatching success.

Infertility was the greatest cause of the differences between pairs and trios in production of offspring. Fertility of eggs laid in double-nests (66%) was significantly lower than pairs (100%) (Fig. 1).

In the 6 trios in which we knew egg ownership, all the primary females' eggs were fertile. Secondary females laid 12 eggs in these trios; 4 (33%) were fertile, 2 (17%) were infertile, and 6 (50%) were undetermined because they were rotten or could not be collected. Based on these data, the infertile eggs in trios' double-nests were the secondary females.

The second cause of depressed reproductive success of trios was significantly lower hatching success (88%) of trios females' eggs that were fertile as compared to pairs (100%) (Fig. 1). Late laying by the secondary female, movement of eggs between nest cups, and incomplete incubation of both nest cups of a double-nest, contribute to lower hatching success of trios' fertile eggs. Each factor is considered below.

Time of laying by the secondary female was determined for 6 trios. There were 1-17 (mean  $5.7 \pm 5.6$ ) days between laying of the primary female's c-egg and the secondary female's a-egg. Late laying appears to be the result of the primary female and/or the male restricting access to the nest

by the secondary female until incubation of the primary female's clutch has begun. When the primary female's young hatch, the stimuli provided by the chicks induces the secondary female to shift to chick care behavior. Beer (1966) has shown experimentally that the introduction of chicks during incubation will cause such a behavioral shift and we have observed this in the trios for which we have prelaying, incubation and hatching data.

The second factor contributing to depressed reproductive success of trios is the cost of movement of eggs and incomplete incubation. In one trio (trio 81) in which the secondary female laid one day after the primary female, the primary female's a- and b-eggs were moved by the birds into cup 2 and the secondary female's a-egg was moved to cup 1. Both cups were not incubated equally. Although cup 1 of the double-nest was exposed only 0.4% of the time which was comparable to 0% exposure for 10 pairs, the eggs in cup 2 were not incubated 24% of the time.

For incubation of 2 adjacent cups by 3 birds (trios) to equal coverage of 1 cup with 2 birds (pairs), each trio member would have to contribute more time to incubation. We found this did not occur. From 15 min scan data collected from trio 81 we determined that during the time cups of the double-nest were exposed, 39% (44/113) and 58% (66/113) of the time 1 or 2 trio members respectively, were present and not out foraging. In only 3% (3/113) of the intervals were 2 birds gone. Because cup 1 received most of the incubation attention only the eggs in this cup hatched. The male and primary female lost 2 potential offspring indirectly as a result of allowing the secondary female to build a nest and lay eggs.

Although the presence of an extra female in a trio resulted in problems in laying and incubation, the secondary female could provide advantages during the chick stage. An important advantage could be better protection of young while they were susceptible to environmental stress or predation which are important causes of chick mortality (Vermeer 1963). To determine this we compared the percentage of time that the trios' chicks and pairs' chicks were left alone. We found that trios' chicks were left alone  $10 \pm 12\%$  of the time which was not significantly different from the  $17 \pm 9\%$  of the time pairs' chicks were left alone ( $U=171.5$ ,  $P>0.05$ ,  $N=11$  trios and 22 pairs). Therefore we conclude trio-attended young do not receive greater protection from environmental stress and from predation than do pair-attended chicks.

A second possible advantage that a secondary female could provide during the chick care period

**Table 1.** Confidence intervals for pair-wise contrasts in mean ranks,  $E(\bar{R}_i) - E(\bar{R}_j)$  for aggression data. In pair-wise contrasts, difference is significant if the confidence interval does not contain zero

Contrast <sup>a</sup>	Estimate	Lower limit	Upper limit
$\bar{R}_1 - \bar{R}_2$	-23.1*	-37.4	-8.8
$\bar{R}_1 - \bar{R}_3$	6.1	-8.2	20.4
$\bar{R}_1 - \bar{R}_4$	-3.8	-16.6	9.0
$\bar{R}_1 - \bar{R}_5$	24.2*	11.4	37.0
$\bar{R}_2 - \bar{R}_3$	29.2*	14.9	43.5
$\bar{R}_2 - \bar{R}_4$	19.3*	6.5	32.1
$\bar{R}_2 - \bar{R}_5$	47.3*	34.5	60.1
$\bar{R}_3 - \bar{R}_4$	-9.6	-22.4	3.2
$\bar{R}_3 - \bar{R}_5$	18.1*	5.3	31.0
$\bar{R}_4 - \bar{R}_5$	28.0*	16.8	39.2

<sup>a</sup>  $R_1$ =Primary female,  $R_2$ =secondary female,  $R_3$ =trio male,  $R_4$ =pair female,  $R_5$ =pair male

\* Denotes  $P<0.05$

is an increase in food delivery. With 3 birds feeding the same number of young that a pair feeds, trios' chicks could build up more reserves than pairs' chicks. Williams (1980) found that in skuas, trio-attended chicks grew faster and probably were in better condition than pair-attended chicks. We used feeding per chick per hour as an indirect assessment of chick quality. Eleven trios fed their chicks  $0.31 \pm 0.2$  feedings/per/h which was significantly higher ( $U=191$ ,  $P<0.01$ ) than  $0.15 \pm 0.1$  feedings/chick/h by 22 pairs.

#### *Behavioral assessment of contribution to a reproductive effort*

Kruskal-Wallis comparison of aggressive encounters per territory for the different categories of birds, then pairwise contrasts procedure of the mean ranks (Table 1) (Marascuilo and McSweeney 1977), indicated 2 differences (Fig. 2a); 1) pair-males contribute more of the total group aggressive acts than the other 4 categories of birds; and 2) the secondary female contributes less to the groups total aggressive acts than the other 4 categories of birds. Trio male, primary female, and pair female contributions are equivalent.

Feeding rates (Fig. 2b) and time on territory (Fig. 2c) were not significantly different between the 5 categories of birds.

#### *Intragroup behavior*

There exists a large amount of variation in the individual trios regarding the degree of acceptance of the secondary female. In the 11 trios for which we have data, 2 trios cooperated throughout the

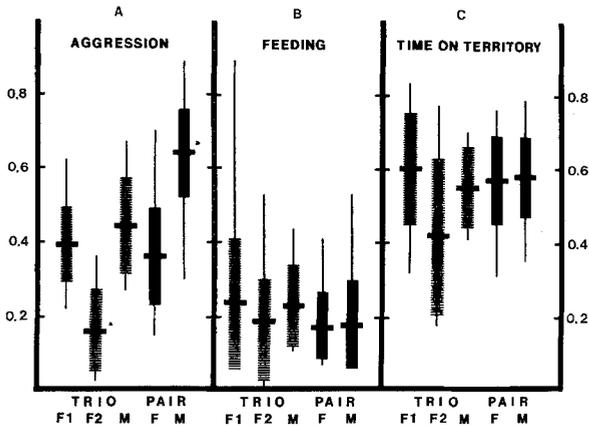


Fig. 2A-C. Behavioral assessment of contribution to the reproductive effort by 5 categories of birds. Means, standard deviations and ranges are indicated. Kruskal-Wallis was used for comparisons. **A** Number of territorial encounters/total performs per territory for 11 trios and 22 pairs.  $H_c = 41.26$ ,  $P < 0.05$ ; secondary females and pair males differed from the other categories of bird (see Table 1 for confidence intervals). **B** Feeding frequency per chick per observation hour,  $H_c = 2.26$ ,  $P > 0.05$ . **C** Proportion of observation time on territory  $H_c = 7.08$ ,  $P > 0.05$ .

entire observation period. In 9 trios, the primary female and male chased the secondary female either throughout the entire observation period (8 trios) or only during pre-laying (1 trio). In these trios the primary female and male directed  $1.07 \pm 1.6$  (range 0.01–5.23) and  $0.7 \pm 1.1$  (range 0.01–3.55) aggressive acts/h, respectively, toward the secondary female. These rates were based on hours of overlap time with the secondary female and are not significantly different ( $T = 25$ ,  $P > 0.05$ ).

The secondary female responded in 67% (323/483) of the total aggressive encounters by simply walking away to the edge of the territory; 14% (70/483) by flying up and relanding in the territory; 13% (62/483) by flying away; 4% (19/483) by letting the male and primary female bite and jab her; and 2% (9/483) pushing or jabbing back. In this respect the secondary female differs from other intruders by persisting in the attempt to associate with the pair and remain on the territory near the nest or young.

The status of primary and secondary females remained the same for 9 trios in 13 between-year intervals. These included 5 trios for 2 successive years and 4 trios for 3 years.

## Discussion

Trios in which both females lay eggs comprised a similar proportion of the breeding groups in the

4 year study period. We believe that most trios form when an unmated female attempts to join a mated male rather than a male mating with a female pair.

A male could increase his reproductive success by mating with 2 females particularly since both females lay eggs. Our comparison of reproductive success using mean yearly reproductive success based on survivorship of young to flying indicates this is not true because of infertility, reduced hatching success, later laying by the secondary female, and incomplete incubation of eggs in the double-nest. Males may derive benefits other than increased yearly reproductive success by association with 2 females, such as, production of better quality offspring because of higher feeding rates, or reduction in the proportion of intruders which they chase from the territory.

Comparison of female reproductive success cannot be based on a simple average because the primary female's offspring are more likely to survive until flying than are the offspring of the secondary female. In the trios for which we were able to establish egg ownership, the primary female produced as many young as a pair female.

There are additional costs and benefits to trio females which pair females do not have. Because most of the young raised by a trio are the primary female's, she benefits by having a secondary female assist in the feeding of her offspring. The benefits provided by the secondary female are offset partially by the costs which include increased energy demand to deter the secondary female in trios which do not cooperate, loss of male assistance, movement of eggs between cups, and incomplete incubation of both cups.

For a secondary female the costs of joining a mated male include overcoming resistance by the primary female and male, late laying, and poor hatching success. These costs are high relative to a pair female's or a primary female's costs particularly because the secondary female receives little compensation in production of offspring.

Previous theories dealing with polygyny suggest that costs of secondary status to a female must be offset by an increase in fitness (Orlans 1969). Based on annual reproductive success the secondary female does not benefit by mating with an already mated male. Secondary status could still be adaptive if the secondary female benefits from increased survivorship which allowed her to breed for additional years (Elliot 1975).

To assess the effects of secondary status on survivorship, we used indices of time and energy which are to some degree commensurate with sur-

ivorship. We found that secondary females did not differ from the other categories of birds in the number of times they fed offspring or in the proportion of their time spent on the territory where activities such as incubation, brooding, and defending the offspring were performed. Secondary females did chase a lower proportion of the intruders away than did the other 4 categories of birds. A lower contribution to defense may make it less expensive for the secondary female to take part in the breeding attempt. However, feeding offspring and spending time on the territory, suggest to us that secondary females are spending almost as much time and energy by associating with a mated male as they would in a typical breeding attempt. Assuming that time and energy expended are negatively correlated with survivorship, it is unlikely that secondary females live long enough to produce sufficient young at the low rate at which they produce young to make breeding as a secondary female over a female's lifetime adaptive.

We assumed throughout this paper that a female has the option of obtaining a male when a female reaches reproductive age, then mating with him in successive years. However, if there are too few breeding males, as has been suggested for Jackdaws (*Corvus monedula*, by Roell 1979), Hen Harriers (*Circus cyaneus*, Balfour and Cadbury 1979), Marsh Harriers (*Circus aeruginosus*, Altenburg et al. 1982), and several gull populations (Hunt et al. 1980; Shugart 1980; Burger and Gochfeld 1981) perhaps females must wait for a male to become available.

Roell (1979) suggested that an operational skew in the sex ratio in a colony of Jackdaws was induced by nest-site limitation. Breeding as a pair was the optimal method because of environmental constraints related to food availability (Roell 1979). He believed that unmated females had the best opportunity to obtain a suitable mate if they remained in the colony. Joining a pair or associating with another female who lost a mate during the breeding season were behaviors which permitted the unmated females to remain in the colony.

A resource necessary for breeding in seabirds is a nest-site. An operational skew imposed by limitation of suitable nesting area in certain regions might conceivably result in females attempting to breed with an already mated male. We are fairly certain this does not apply to the northeastern region of Lake Michigan because the Herring Gull population has increased since 1976 by about 10% per year with no significant increase in nesting area (Shugart unpublished data) which indicates that

sufficient nesting area was available when we first began investigation of this phenomenon.

Although there does not appear to be an operational skew due to nest-site limitation in our study area, there may be an actual skew in this area (Shugart 1980; Shugart and Fitch, in preparation) and other gull populations (Hunt et al. 1980; Fry and Toone 1981). Sex ratio skews in gull populations could be natural because there may be a tendency for greater female survivorship in seabird populations (Wooller and Coulson 1976; but for the Herring Gull see Chabrzyk and Coulson 1976). This tendency may be magnified by unnatural factors such as physiological differences between sexes in lipid and lipophilic toxic chemical dynamics (Shugart 1980; see also Fry and Toone 1981). Unlike other avian species in which joining an already mated male is adaptive due to an operational or actual skew in the sex ratio (Holm 1973; Carey and Nolan 1975; Pleszczynska 1978), we have shown that in the Herring Gull, as in the Pied Flycatcher (*Ficedula hypoleuca*, Alatalo et al. 1981) and the Marsh Harrier (Altenburg et al. 1982), secondary status is not adaptive based on annual reproductive success. Why then are females associating with mated pairs for long periods of time? The annual reproductive success of a secondary female could increase if the primary female died or if the secondary female became familiar enough with the male to breed as the primary female in subsequent years. Although replacement did not occur in the 2 to 3 years we studied trios, in species in which individuals are long-lived such as the Herring Gull replacement may occur over a longer period of time. If this is true, joining a mated male may maximize lifetime reproductive success if there are too few males in the population.

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