

Unequal Sex Ratios and Their Consequences in Herring Gulls (*Larus argentatus*)

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Summary. We observed the sex ratios and age composition of courting, nesting, and nonbreeding birds (in clubs) in four breeding colonies of Herring Gulls in Maine and New York. Breeding pairs, with eggs or chicks, often contained an immature male, but rarely contained an immature female. Similarly, courting pairs contained immature males, but rarely immature females. A higher proportion of courting pairs contained immatures compared with pairs with eggs or chicks. In all four colonies there was an excess of females in the clubs. A simulated colony which assumed unequal survival for males and females had an age ratio for unpaired birds that was similar to the observed values. We conclude that in Herring Gulls, mate competition exists and stems in part from an unequal tertiary sex ratio.

Introduction

The evolution of avian mating systems has received considerable attention. Until recently, seabirds were considered monogamous (Lack 1968). However, new data on seabird mating systems have yielded new insights into the complexity of their social systems (see discussion in Hunt 1980; Fitch 1980). Although evidence still points to monogamy as the predominant pair bond type, polygyny, female-female pairing, and promiscuity have been noted for gulls (Shugart and Southern 1977; Hunt and Hunt 1977; Conover et al. 1979; Ryder and Somppi 1979; Fitch 1980); and polygyny has been reported for skuas (*Catharacta*; Bonner 1964). However, in gulls and skuas the incidence of mating systems other than monogamy is very low (see Fitch 1980). Darwin (1871) invoked uneven sex ratios as an explanation for polygyny, and this remains one possible explanation of nonmonogamous mating in birds (Verner 1964, Altmann et al. 1977).

However, most students of polygyny in those altricial species that are predominantly polygynous (Verner 1964; Orians 1969); Wittenberger 1976) do not attribute such mating systems to uneven sex ratios, and for most species that have been adequately studied there is no evidence of significant departure from equality in the sex ratio at fledging (Orians 1969).

Hunt (1980) reported that Western Gulls (*Larus occidentalis*), for which female-female pairing has been reported, have a ratio of 0.67 males: 1 female based on the frequency of female-female pairs, ratio of nonbreeding females to males in clubs, and the total number of birds in the colony. Hunt et al. (1980) suggest that this uneven sex ratio in Western Gulls may have a causal role in the formation of female-female pairs. Similarly, Mills (1973) found an excess of female Red-billed Gulls (*L. novaehollandiae*) in breeding colonies. Females often had difficulty finding mates; three-year-old females sometimes bred with two-year-old males, although the reverse was not observed. In Black-legged Kittiwakes (*Rissa tridactyla*), males breed on average a year earlier than do females (Wooller and Coulson 1977), and male kittiwakes have lower survival rates than do females.

In this study we examine the sex ratios of Herring Gulls (*L. argentatus*) breeding in colonies in New York and Maine. If male Herring Gulls have lower survival rates than females, then there should be an excess of females in colonies. Such an excess of females should lead to more intense competition for mates among females compared to males, resulting in young males being more than able to obtain mates young females. This study was designed to test the following predictions: (1) a high proportion of immature males should be breeding compared to immature females, (2) late courting pairs should contain more immatures than already established pairs with eggs or chicks, (3) late courting pairs should contain more immature males than immature females, and (4) the

nonbreeding birds on clubs seeking mates should contain an excess of females compared to males. Also, using Wooller and Coulson's (1977) survival figures for male and female kittiwakes, we simulate a theoretical sex ratio for a gull colony, and compare this with field data.

Material and Methods

We examined sex ratios and age composition of Herring Gulls (*Larus argentatus*) breeding on Appledore Island (Isles of Shoals, Maine); and at Captree, Meadowbrook, and Meadow Island on Long Island (New York) in 1980. All colonies contained Herring (HG) and Great Black-backed Gulls *L. marinus* (GBB): Appledore (1,800 HG:750 GBB nests), Meadowbrook (600 HG:5 GBB), Meadow Island (500 HG, 3 GBB), and Captree (1,200 HG:100 GBB). In the New York colonies Herring Gulls nested on sand in *Ammophila* beachgrass while on Appledore Island the gulls nested on rocky outcroppings on grassy knolls.

In all colonies we determined the sex and age of: breeding pairs (those with eggs or chicks), courting unpaired birds in clubs, and paired birds still courting in the clubs. The late couples may or may not attempt to breed in the current year. We determined sex visually by comparing the members of a pair (for paired and courting pairs), and by comparing adjacent birds for unpaired birds. In many gulls, particularly in Herring Gulls, males are significantly larger in body size and bill measurements (Ingolfsson 1969; Bianki 1977; Shugart 1977). Although there is 2–11% overlap in any one measure in gulls (Ingolfsson 1969; Shugart 1977; Ryder 1978), the combination of overall size, bill length, and bill depth allows accurate sexing. Shugart (1977) developed a sexing formula that could be accurately used in the field for Herring Gulls, which made use of the combined head and bill measurement. Using his formula, over 98% of the Herring Gulls were classified correctly (Shugart 1977). Therefore, we used head and bill as an indication of sex, and checked our identifications against copulation position where possible. Further, by comparing within couples the identification is positive since males select smaller females. We sampled all pairs with eggs or chicks on the central area of the colony unless otherwise specified. In courting pairs, sex was determined by copulatory position.

In Herring Gulls immatures (three and four year olds) have a partial tailband, although there is considerable variation in the age at which gulls first possess an all-white tail (see Dwight 1920, 1925; Poor 1946; Monaghan and Duncan 1979; Schreiber and Schreiber 1979). We assume that birds with a partial tailband are immatures and are younger than birds with an all-white tail. Some immatures had entire tail bands, while others had only dark spots on two or three tail feathers.

To simulate a colony we used the annual survival figures for Kittiwakes provided by Wooller and Coulson (1977): females, 1–5 years=0.86, 6–17 years=0.78; males, 1–5 years=0.83, 6–17 years=0.75. Every year for 15 years we added 1,000 one-year-old males and 1,000 one-year-old females; and computed the proportion of each sex that would still be present at the end of the 15 years.

Results

In examining nesting pairs we found that males were incubating or brooding more often than females (Table 1). However, nonincubating birds were often present at the nest, and females slightly outnumbered

Table 1. Number of birds breeding and courting, and sex and age composition as a function of stage in reproductive cycle

	New York			Maine
	Captree	Meadow Island	Meadow brook	Appledore
Breeding pairs^a				
Total number nests	82	142 ^d	67	82
% with males incubating or breeding	54 ^e	55	58	60
% females incubating or breeding	46	45	42	40
% of pairs with Immatures	8	17	12	20
% male	100	92	87	88
% female	0	8	13	12
Club birds^b				
Total number birds	55	76	44	46
% males	38	37	36	46
% females	62	63	64	54
% Immatures	15	24	18	30
% male	50	43	50	43
% female	50	57	50	57
Courting, paired birds^c				
Total number pairs	20	18	4	8
% with at least one Immature	50	22	50	38
% males	100	100	94	100
% females	0	0	6	0
Habitat for courting	Open sand	Open sand	Open sand	Roofs

^a Nests with eggs or chicks

^b All birds in the club that were engaged in courting or approaching other birds

^c Only those pairs actively courting as pairs

^d All had chicks

^e The unequal percentage of males indicates that males were present and incubated more often than females. Therefore, the nonincubating mate was more often the female. Both sexes were present at the nest an equal percent of the time

males as nonincubators. The percentage of breeding pairs having one immature was 8–20%; males comprised 88–100% of these immatures (Table 1). We found only one pair (at Appledore Island) where both members of a pair were immatures: the male had an all-black tail band whereas the female had black on only two tail feathers. As might be expected, edge areas of the colony contained a higher proportion of immature nesting birds. For example, at Captree, in an area known to be colonized recently (within 3 years, D.B. Ford, personal communication), 22% of the pairs contained an immature male (no immature females), whereas in a central area only 5% had immature males.

Non-nesting Herring Gulls often gather in clubs, and even in June many are still seeking mates (Tinbergen 1963). In all clubs examined, there was an excess of females (mean 62.2%, see Table 1). This difference

Table 2. Age and sex of Herring Gulls in a simulated colony based on differential mortality of males and females. Population based on the 15th year, after annual introduction of 1,000 one-year-old males and 1,000 one-year-old females

	Total population	Four years and older	Excess adults ^a	Three year olds ^b	Excess breeders ^c
Males	4,910 47%	2,391 45%		689 48%	—
Females	5,561 53%	2,961 55%	571 ^b	740 52%	622
Total	10,471	5,352		1,429	

^a Potential for 571 adult females to mate with three-year-old males, yielding 19% of the total 2,961 pairs

^b Potential for 1,429 three year olds plus 571 adult females to be on clubs, either courting or unpaired

^c If all above birds pair, then 622 females will be left without mates

was significant in all colonies except Appledore Island (χ^2 -test) where Herring Gulls are decreasing. For this analysis we counted all birds that were in the club whether they stood singly (and approached other birds), in pairs, or in groups of three or four (usually only one male to a group). We often observed a female approach a courting pair, and the intruding female solicited (head-tossed) to the male. The paired female usually chased the intruding female. In all colonies, clubs had a higher proportion of immatures than were nesting in the adjacent colony, (Table 1) (significant at $P < 0.025$ at all colonies except Meadowbrook). The ratio of immature males to immature females was nearly equal in the clubs. This is expected if there is only a slight sex difference in mortality each year. However, among immatures in clubs, those that were part of actively courting pairs were nearly all males (49:1).

In all colonies there was an excess of females in the courting groups. We therefore simulated a Herring Gull colony using Wooller and Coulson's (1977) estimates for kittiwake survival (see Material and Methods). We assumed an equal number of one-year-old male and females. At the end of 15 years our simulated colony contained 10,471 birds (53% females). There were 2961 females of four years and older compared with 2391 males of four years and older, or an excess of 571 females. If each of these paired with an immature three-year-old male, then 571 of the resulting 2961 pairs (19%) would have one immature bird. This is very close to the observed values (8%, 12%, 17%, 20%). Assuming that three-year-old males and females and the excess of older females participate in courting in the clubs, then there would be 1311 females and 689 males, a ratio close to those actually observed (females comprising 62%, 63%, 64% and 54% in the four colonies). The simulated colony has 65.5% females in the clubs, only

slightly higher than the maximum observed in the real colonies (Table 2).

Discussion

In all the Herring Gull colonies we examined there was an excess of gulls that were not engaged in breeding. The causes of gulls not breeding are many and varied (see Mills 1973; Hunt 1980). Nonetheless, in this study there was an excess of females at the breeding colony, and immature males bred and courted actively whereas immature females generally did not. The consistency of these results among colonies is noteworthy, and suggests that competition for mates may be relatively strong in females, whereas all adult males find mates, and most three-year-old males are potentially capable of obtaining mates. Competition for mates is a cost of reproduction often alluded to (see Hunt 1980), but it is difficult to document. The courting and pairing clubs common in gulls provide excellent opportunity to study this phenomenon. However, marked birds are essential for such a study.

Immature males clearly are able to breed successfully, as all immature birds in the breeding category had eggs or young. At Meadow Island where all breeding birds had young we found no differences in mean brood size for immatures ($\bar{x} = 2.11 \times 0.6$) compared to adult males $\bar{x} = 2.62 \pm 1.2$, t -test, $df = 37$), and immature males had chicks which were as old, indicating that some had bred early. Similarly, males with tail bands were actively engaged in brood defense, and seemed equally likely to chase another gull that approached the brood too closely.

In a 2-h observation at Meadow Island, four immature males had aggression rates (No. chases/h) of 3.2, while adult males had aggression rates of 3.5. Although preliminary, these results suggest only slight differences in brood size and in aggressive behavior. However, additional sampling might indicate significant differences. Ryder (1975) also found that immature male Ring-billed Gulls *L. delawarensis* bred with adults and that immature females were found breeding only in pairs where both birds were immature. Mills (1973) found that the male was the younger member of a pair in 57% of 212 pairs of Red-billed Gulls, but he was not only examining immatures plumaged birds. The overall importance of mate competition was not stressed in either paper. Their results, and those reported herein, suggest that competition for males by females is an important component of the mating system in gulls.

The discrepancy between the ratios we found for nonbreeding birds compared to the simulated colony may reflect that the colonies examined are still expanding. In an expanding colony each succeeding age

cohort would be larger, and some of the excess of older females could be absorbed by the larger three-year-old male cohort. Hunt (1980) proposed that in an expanding population the excess of older females could breed with younger males resulting in no excess of females. However, since for any given year females outnumber males, there would always be an excess of females (in the case of the model, three year olds), which would be unable to breed.

Emlen and Oring (1977) have defined an operational sex ratio (based on the number of individuals of each sex actually available for breeding at any time and place), which they invoke as an important determinant of mating systems. Our observations suggest that breeding Herring Gulls, at least in certain colonies, experience an operational sex ratio in which females outnumber males, and in which adult females accept immature males as mates. This carries with it a disadvantage, in that many studies have shown that younger birds of either sex experience lower reproductive success than older ones (Mills 1973). We suggest, however, that gull biologists need to determine if attempting to breed at an earlier age decreases survival, and if birds that attempted to breed as immatures are more successful as adults than gulls without such experience.

Assuming equal sex ratios at fledging (an assumption still needing proof), differential survival must result in an excess of the sex with higher survival, and should lead to intense mate competition for the rarer sex, to differential ages of breeding, or to alternative mating systems such as polygyny or female-female pairing (where females mate promiscuously to fertilize their eggs). Indeed, Hunt et al. (1980) found similar unequal sex ratios in Western Gulls in California, and suggested that the unequal sex ratios might have a causal role in the formation of female-female pairs. To date no one has reported female-female pairs on the Atlantic Coast of North America despite the apparent unequal sex ratio. In all the colonies we examined we did not find any six-egg clutches (indicative of female-female pairs) or double nests (indicative of polygynous groups in the Great Lakes, Shugart and Southern 1977). Thus monogamy still seems to prevail on the East Coast, and the unequal sex ratio seemed to be reflected in the age of first breeding.

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