

We could find no reports of this or any other species of *Parus* excavating a cavity on the underside of a horizontal limb. This location would seem to make the nest less vulnerable to predators than the more typical cavity in a vertical position.

Haartman (1957) noted that in hole-nesting birds, a number of convergent adaptations occur, mainly those functioning to reduce predation and intra- and interspecific competition. For example, snake-like hissing occurs in many parids and some other unrelated hole-nesters (Hinde 1952, Haartman 1957). Bill-sweeping has been described in detail by Kilham (1968) in the White-breasted Nuthatch, and the behavior is similar in many respects to what we observed in the chickadee. The area around the nest is swept or dabbed by objects in the bill, primarily crushed beetles, although nuthatches also use fur, feathers, and plant material. Kilham (1968) speculated that crushed beetles contain repellent substances, and identified blister beetles, *Meloe angusticollis*, as the probable source (Kilham 1971). Nuthatches intensified sweeping when squirrels were near the nest. Kilham (1968) suggested that the sweeping may reduce nest competition; however, as squirrels may also be nest predators, we suggest that the behavior may reduce predation. For the Mexican Chickadee, which excavates its own nest, and the cavity is quite small, most likely sweeping is directed primarily at potential predators rather than interspecific competitors. Kilham (1968) had suggested that bill-sweeping may be unique to the White-breasted Nuthatch; the

closely related Red-breasted Nuthatch (*Sitta canadensis*) applies sap to the vicinity of the nest but is not known to sweep.

Despite numerous studies of nesting parids (e.g., reviews of Hinde 1952, Perrins 1979), bill-sweeping has never been reported previously. We speculate that in the Mexican Chickadee sweeping may be a response to unusually heavy predator pressure by the numerous small mammals and reptiles in its montane habitat. Bill-sweeping is thus another example of convergent behavioral evolution in hole-nesters.

We thank C. M. Weise and K. Apel for their comments. Publication No. 96 of the University of Wisconsin-Milwaukee Field Station.

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The Condor 89:902-906
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FEMALE FLOATERS AND NONBREEDING SECONDARY FEMALES IN HERRING GULLS¹

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Key words: Larus argentatus; gulls; sex ratio; floaters; secondaries; female pairs; female competition.

A small portion of gull nests contain supernormal clutches either in single or double nests (see Conover 1984 for review). Behavioral studies of attendants at

these nontypical nests indicate that a breeding (i.e., egg laying) secondary female or a female pair usually is involved (Hunt and Hunt 1977, Fitch and Shugart 1983, Kovacs and Ryder 1983). Apparently, these females are attempting to breed after failing to heterosexually pair. This interpretation is supported by the occurrence of female pairs/secondary females in populations with male shortages (Hunt et al. 1980, Conover and Hunt 1984, Coulson and Thomas 1985) and successful rearing of offspring by female pairs/secondary females (Fitch and Shugart 1983, Kovacs and Ryder 1983).

¹ Received 3 October 1986. Final acceptance 22 April 1987.

While studying behavior of female Herring Gulls (*Larus argentatus*), in addition to breeding females, we observed what appeared to be nonbreeding secondary and floater females. To document their existence, we provide quantitative description of nonbreeder behavior. We then consider how nonbreeding status relates to breeding statuses by examining the relative frequencies of the statuses and demographic basis.

METHODS

The study was conducted primarily at the 2,500-nest Herring Gull colony on Gull Island National Wildlife Refuge in northeastern Lake Michigan, hereafter (LM), during 1981 and 1982. Additional sites used for sex ratio research were nearby Squaw Island (105 nests) and Bellows Island (1,000 nests) (see Shugart 1980), and Gull Island in eastern Lake Ontario, hereafter Gull Island (LO). There were breeding groups other than heterosexual pairs from 1978 to 1981 at all study sites (Shugart, Fitch, and Fox, unpubl. data).

All individuals used for this study had been color-banded in other studies, or we temporarily marked them using a Nel-Spot paint pistol (see Fitch and Shugart 1983, 1984). Birds were in adult plumage (see Dwight 1925) unless otherwise noted. At each study area, numbered stakes placed at 3-m intervals formed grids for mapping territory boundaries and birds' locations.

We quantified behavior using scan and focal sampling (see Altman 1974). In scan sampling, individual birds' locations and behavior were recorded at 15-min intervals. In focal sampling, an individual was observed and behavior was continuously recorded. Observations were done at three study areas, which were designated north, east, and south, on Gull Island (LM) in 1981 and 1982. Observations were done 5 to 6 days per week from laying (late April) until fledging (late July) with the exception of the first week of May 1982. Hours of sampling and the periods that behavioral sampling were conducted differed for different questions. Specifics are presented with data in Results, Figure Legends, or parenthetically in the text.

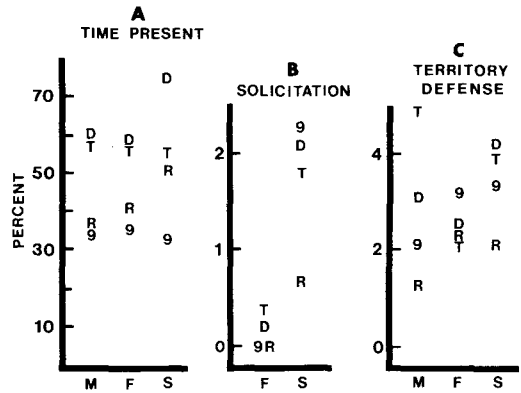


FIGURE 1. Comparison of NB secondary female (S), male (M), and primary female (F) in respective pairs (D, T, R, and 9). Hours of data collection per pair: D, 173.5; T, 198.5; R, 139.8; and 9, 130.5. A. Percent time on territory was not significantly different (Kruskal-Wallis $H = 5.7$, $P > 0.1$). B. Rate of soliciting to male by NB secondary female was significantly higher than primary female ($U = 16$, $P = 0.025$). C. Percent of time present in territory defense was not significantly different ($H = 1.9$, $P > 0.5$).

We examined the tertiary sex ratio at study colonies using cannon-netting and removal experiments. In the former, the net was fired over loafing areas within 5 min of spreading bait in front of the net (see Hunt et al. 1980). Captured birds were sexed (Fox et al. 1981), color-banded, and examined for brood patches. We timed our cannon-netting to coincide with the fourth week of incubation at the respective colonies. Therefore, if a bird did not have brood patches at this time, we categorized it as a nonbreeder (Hunt et al. 1980).

Removal experiments indicate if there were unpaired birds of either sex in study colonies (Stewart and Aldrich 1951, Hannon and Zwickel 1979, Saether

TABLE 1. Hourly rates of agonistic interaction between nonbreeding secondaries and pair members. Rates are based on hours of opportunity during 4 weeks centered at hatching (see footnotes).

	T	R	9	D
Total observation time (hr):	80.25	70.25	60.00	71.75
Aggression (hr ^a):				
Male	0.58 (16)	0.29 (14)	0 (12)	0.01 (23)
Female	0.85 (22)	0.87 (17)	1.95 (9)	2.56 (24)
Sexual behavior (hr ^b):				
Male	0.68 (19)	0.57 (30)	0.40 (15)	0.63 (30)
Female	0 (28)	0 (29)	0 (15)	0.03 (30)
Nest building ^c :				
Male	0.32	0.06	0.13	0.77
Female			0	

^a Female aggression rates greater than male ($U = 16$, $P = 0.025$). Time available for aggression (hr) when males or females on territory but not on nest and NB secondary present.

^b Time available for interaction (hr) NB when secondary on territory, male or female alone on nest with mate absent, or male or female standing on territory with mate on nest.

^c Time (hr) available is same as for sexual behavior.

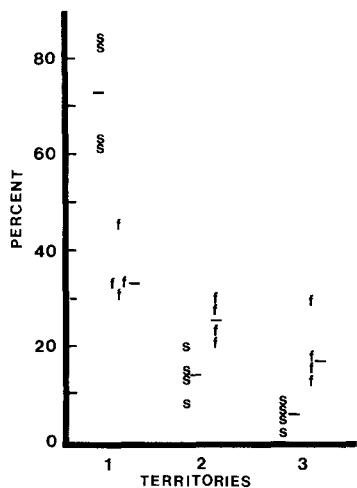


FIGURE 2. Percent of time present ranked by distribution on multiple territories by nonbreeding secondary (s) and floater (f) females in 1981. Distribution of floaters' occurrences show greater evenness than the distribution of NB secondaries. NB secondaries and floaters were significantly different for three categories ($U = 16, P = 0.05$).

and Fonstad 1981, Picozzi 1984). We removed one member of a sample of pairs during the second or third week of incubation. Eggs were collected from the experimental birds' nests upon removal of the mate. Thereafter, at 3- to 4-day intervals in 1981, and 7-day intervals in 1982, the study areas were searched for signs of nest construction. We then observed the birds attending newly constructed nests and quantified their behavior using scan sampling.

RESULTS

NONBREEDING (NB) SECONDARY FEMALES

NB secondaries include individuals that were present as much or more than the males and females whose territories they frequented (Fig. 1a). In contrast to primary females, NB secondaries spent significantly more time soliciting to the male (Fig. 1b; i.e., head-tossing and begging, see Tinbergen 1953). NB secondaries helped host pairs by defending territories as often as pair members (Fig. 1c). In addition, two of the four (9 and R) fed host pairs' offspring throughout chick rearing.

We are confident that NB secondary females did not lay eggs (i.e., were not breeding secondaries) because primary females' eggs were marked at laying, and only primary females were on nests during the laying period (see Fitch and Shugart 1984). Breeding secondaries lay eggs within 6 days (mean) of the primary female (Fitch and Shugart 1983).

In the absence of egg laying, NB secondary status provides no obvious immediate reproductive benefits. In fact, NB secondaries were subjected to considerable aggressive harassment, especially from primary females who chased NB secondaries out of, or around the territory, at a significantly higher rate than males

TABLE 2. Frequency of female Herring Gull statuses at nests in sample areas of Gull Island, Lake Michigan.

	Frequency/No. of nests (%)	
	1981	1982
Breeding statuses:		
Secondary female	7/112 (7.1)	5/103 (4.9)
Female pair	2/112 (1.8)	3/103 (2.9)
Subadult male	1/112 (0.9)	1/103 (1.0)
Nonbreeding statuses:		
Secondary	8/112 (7.1)	5/71 (7.1)
Floaters	1 per 5 territories (22 territories mapped)	

(Table 2). Despite primary females' interference, NB secondaries persisted in approaching males and engaged in sexual and nest-building activities when primary females were absent or on nests (Table 1).

FLOATERS

Four individuals were used to provide the quantitative description of this status. Three of these were females based on measurements (Fox et al. 1981), and the fourth was judged to be a female based on comparison of size to known males (see Burger and Gochfeld 1981). This quantification is based on the following observation hours, year, blind: 214, 1981, west; 198, 1981, east; 223, 1982, west; 155, 1982, east.

The four floaters were present in the study areas 33 and 42% (medians) of the time in 1981 and 1982, respectively. This represents a considerable portion of time and indicates floaters' occurrences in territories were not incidental. For comparison, floater time present was significantly less than paired females' 51% of time 1981 ($U = 56, n_1 = 4, n_2 = 14, P = 0.001$), but not different from 43% time present in 1982 ($U = 15, n_1 = 4, n_2 = 7, P > 0.2$).

Floaters differ from NB secondaries in that the former spent significantly less time in a single territory (Fig. 2). This difference reflects repeated displacement of floaters by territory owners. The four floaters were intruders in 5%, 10%, 14%, and 16% of 1,524 incidents of territorial aggression recorded for 10 breeding pairs (data from 1981).

Despite repeated displacement by residents, floaters remained in the study areas by moving to another territory rather than leaving the area. We documented this movement using focal samples (23 samples, total time = 1,697 min, median length = 50 min). In 350 interterritory movements, we found that a floater moved to another territory every 6.5 (median) min. Sixty-five percent (226/350) of these interterritory movements were in response to territory owners' aggression. In 64% (145/226) of these, floaters walked or ran to an adjacent territory while in the remaining 36% (81/226), the floater flew. In the latter case, the floater circled and landed back in another territory in the study area rather than in another portion of the colony. Interterritory movement continued until the floaters entered a territory where the breeders were absent, sleeping, or did not chase them.

The remaining 35% (124/350) of floaters' interter-

TABLE 3. Success of experimentally widowed male and female Herring Gulls in obtaining new mates. Of the total subjects (*n*), the number in each column indicates: new pairs that produced eggs (Eggs); formed new pairs without laying eggs (Pair); and present in the colony, but did not form a new pair (Present).

	Males (females removed)				Females (males removed)			
	<i>n</i>	Eggs	Pair	Present	<i>n</i>	Eggs	Pair	Present
1981								
Gull Island, Lake Michigan	10	5	3	2	9	0	0	8
1982								
Squaw Island, Lake Michigan	8	5	1	2	8	0	0	5
Gull Island, Lake Ontario ^a	5	2	1	2	5	0	0	2

^a Sample size was originally 8, but three experimental males that paired with three experimental females are excluded.

ritory movements were initiated by floaters. Of these, 26% (32/124) occurred as floaters threatened other birds. In aggressive encounters initiated by floaters, other floaters were the stimulus 58% of the time, unmarked individuals 38%, and NB secondaries and territory owners 4%. In the infrequent encounters in which floaters threatened residents or secondaries (2/166), the floater was displaced. However, in 99% (164/166) of the encounters with floaters and unmarked birds, the floater that initiated the encounter displaced the intruder.

RELATIVE FREQUENCY AND STABILITY OF STATUSES

The above quantification confirms that females of nonbreeding status were present in colonies. By using the above criteria to identify nonbreeders, and criteria for breeders in Fitch and Shugart (1983), Shugart (1980), and Burger and Gochfeld (1981), we determined the relative frequency of statuses (Table 2). From this summary, it is evident that all statuses occurred simultaneously in the colony. With the exception of the predominant status, heterosexual pairing with an adult male, nonbreeders were as frequent as breeder statuses.

We followed individuals within and between breeding seasons to determine if individuals' statuses were stable. For within seasons, we marked the samples of individuals in Table 2. All but one female, a NB secondary that paired with an unmarked female, remained in the same status during the reproductive season. A smaller sample of these females were color-banded, which allowed us to follow them in consecutive years. Of eight breeding secondaries and nine females in female pairs, only one changed status (breeding to NB secondary). Two of five nonbreeders changed to other statuses including a floater to a heterosexual paired female and a floater to female pair status.

TERTIARY SEX RATIO AT BREEDING COLONIES

Of adults captured in cannon-netting, at Gull Island (LM) nonbreeders comprised 12% (5/41) of the males and 32% (22/68) of the females ($G = 4.9$, $P < 0.05$). Four percent (1/23) of the males and 68% (15/22) of the females were nonbreeders at Bellows Island ($G = 19.3$, $P < 0.001$). The significantly smaller proportion of the nonbreeding males than females on both islands

as well as the greater number of nonbreeding females captured is evidence that there was a surplus of adult females at the study colonies.

Additional evidence of excess females was provided by removal experiments. We found that 68% (16/23) of the males paired with new females while none of the females paired with nonexperimental males (Table 3). This difference was not an artifact of the female's inability to re-pair because three experimental females paired with experimental males (Table 3). Sex differences (i.e., males remain on territory, females seek out males) in re-pairing behavior can also be excluded as an explanation. In 1981, widowed females remained on or near their territories (Table 3), while in 1982, colonies were small enough to allow us to locate new nest construction associated with new pairs (Table 3).

DISCUSSION

Data from cannon-netting and removal experiments indicate that a shortage of breeding males exists at our study colonies. This shortage provides the demographic context for the female statuses other than heterosexual pairing with an adult male.

Females' statuses typified by attempting to breed, either as secondaries, in female pairs, or by pairing with a subadult male, provides a point of contrast to the NB secondaries and floaters that we described in this paper. The breeding statuses could provide immediate, albeit minimal, reproductive benefits (Fitch and Shugart 1983, Kovacs and Ryder 1983, Chabrzyk and Coulson 1976) whereas nonbreeding statuses do not appear to provide any immediate benefit. In relation to breeding statuses, NB secondaries may be attempting to attain secondary breeding status and floaters may represent an initial step in establishing secondary status. An alternative interpretation, which emphasizes future reproductive benefits, is that floating (see Smith 1978) and NB secondary status (see Reyer 1980) are waiting strategies. By not becoming involved in minimally successful breeding attempts, these females may be able to take advantage of heterosexual pairing opportunities should one become available in the area they frequent.

We thank the personnel of the U.S. Fish and Wildlife Service for research permits on Gull Island (LM). This research was partially supported by NSF doctoral dissertation grant #BNS-800-07582 to Fitch and by the

Canadian Wildlife Service. Shugart prepared this paper while a NSF post-doctoral fellow in environmental biology (BSR-8503050).

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