

**COPULATORY WING-FLAGGING:
A SYNCHRONIZING STIMULUS FOR NESTING
RING-BILLED GULLS¹**

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The courtship behavior of various species of *Larus* gulls has been described in detail by Goethe (1937), Tinbergen (1960), and others. Most authors have discussed courtship in general or stressed pre-coition displays, and far less attention has been given to the possible functions of the rhythmic wing movements and vocalizations of copulating gulls. Tinbergen (1960) considered the wing movements during Herring Gull (*L. argentatus*) copulation to be for balance only, which was probably their original function, and is to some extent a continuing function.

Brown (1967), Emlen and Miller (1969), and Immelmann (1971) reported that performance of courtship or nesting behavior by one pair or groups of pairs can stimulate other pairs to do the same, thereby resulting in synchronization of activities.

During this study I compared the behavior of Ring-billed Gulls near copulating pairs (the experimental group) with that of gulls in the same area during non-copulatory periods on the same days and within the same two-hour span (the control group). By this method I attempted to determine if certain stereotyped actions associated with copulation caused an alteration in the ongoing behavioral sequences and a contagious increase in the frequency of copulatory behavior. Such a response would contribute to synchronizing the breeding cycle within the colony. Copulating pairs are obvious because of vigorous ritualized wing-movements, unique vocalizations, and exhibition of the male's bright orange gape.

METHODS

During March through May of 1967 and 1968, I spent several weekends in a Ring-billed Gull colony near Rogers City, Presque Isle County, Michigan. During this time I observed courtship behavior, particularly copulation, and recorded the reactions of nearby birds. Because it was difficult to watch a sufficient number of birds and to record their individual reactions during each copulation, I filmed these activities with a 16mm Bolex Camera equipped with a zoom-lens. Whereas this approach was superior in some ways to direct observation, it also had limitations since it was usually impossible to film a complete courtship and copulation sequence without rewinding the camera.

Twenty-two of the filmed copulations and 22 control periods of non-copulatory activity of equal duration have been analyzed for this paper. The sequences ranged from 0.51 to 2.5 minutes in length. The films were viewed with a LW Motion Analyzer Projector.

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The full significance of this display is difficult to quantify since it is impossible to ascertain under field conditions if neighbors, that witness copulation without showing overt responses, are actually exhibiting endogenous responses. In my attempt to determine if a change occurred in the preponderance of any activity performed by neighbors during, or immediately following copulation, I listed the behavioral activities of all gulls within approximately a three-meter radius of the mating pair. After listing the activities observed on film, I again viewed the films and quantified the responses (Table 1). The results from the experimental and control groups were contrasted in an attempt to determine if copulation by one pair induced mating activity by nearby individuals after a period of abstention from such behavior. The chi-square test with Yates correction for continuity (Zar, 1974) was used to indicate goodness of fit. All of the 13 broad behavioral patterns used as indicators are not directly associated with copulation; instead they were selected because of their obviousness and are used to show that the overall type and rate of activity is different following Wing-flagging.

The following 13 behavioral patterns were recorded and their frequency of occurrence tabulated:

Agonistic responses. These are various types of threat or aggressive actions, including head thrusts at the Wing-flagging bird, pulling of the male's outstretched wings, and interactions between adjacent individuals.

Walking toward. Includes movements by members of nearby pairs, ranging from a few steps to covering distances of several meters that either resulted in turning toward the copulating pair or movement closer to them.

Preening. This was the performance of standard grooming behavior which may or may not have represented displacement activity.

Soliciting. Incorporated head-tossing by females; the circling of a mate; and, open-mouth (premounting) postures by males.

Bill-pointing. May be called nest-pointing and involves one or both members of a pair pointing at the ground and making short bill thrusts thereby marking the site at which a nest depression will be excavated.

Head-tucked. A typical resting-posture where the bill is tucked beneath the scapulars and the eyes often are closed.

Plumage-fluffing. Rearrangement of the plumage by shaking the wings, body, and individual feathers.

Nest Building. Excavating movements or adding nesting materials.

Departures. Includes taking off and flying out of the area by nearby individuals.

Arrivals. Refers to flying into and landing in the area, presumably by neighbors.

TABLE 1.
Frequency of occurrence of the 13 behavior patterns recorded during 22 experimental and control periods of observation.

SESSION NO.	AGONISTIC RESPONSES		MAKING TOWARD		PREENING		SOLICITING		BILL POINTING		HEAD TUCKED		PLUMAGE FLUFFING		NEST BUILDING		DEPARTURES		ARRIVALS		LOOKING TOWARD		VOCALIZING		MOUNTING			
	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.	Exp.	Cont.
1	3	4	10	13	1	6	4	12	0	3	0	0	1	2	0	0	0	0	0	5	6	8	4	6	1	0	0	
2	0	6	1	19	2	12	1	8	0	7	0	0	0	0	0	0	0	0	0	1	6	0	5	4	0	0	0	
3	1	12	4	13	0	6	0	12	0	3	0	0	0	0	0	0	0	0	0	2	10	8	8	6	0	0	0	
4	5	2	7	17	0	13	0	5	0	3	0	2	0	4	0	0	0	0	0	1	7	0	9	0	2	0	0	
5	4	2	2	9	0	12	3	2	0	3	0	2	2	0	3	0	0	0	0	1	7	0	5	2	1	0	0	
6	1	2	2	9	0	5	1	5	0	2	0	1	0	2	0	0	0	0	0	0	5	0	3	1	4	0	0	
7	0	0	2	8	4	7	0	3	0	0	1	1	0	0	0	0	0	0	0	0	4	0	2	0	0	0	0	
8	0	0	1	8	0	2	0	3	0	2	0	1	1	2	0	2	0	0	0	0	0	0	3	0	0	0	0	
9	0	1	3	13	1	7	3	1	4	0	0	1	1	4	0	4	0	0	0	1	7	0	4	2	0	0	0	
10	1	0	0	11	4	2	2	1	0	0	0	0	0	2	0	0	0	0	0	1	9	0	5	1	3	0	0	
11	0	11	4	12	0	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	9	0	5	0	2	0	0	
12	0	1	5	1	3	2	2	0	0	4	0	5	0	6	0	3	0	0	0	0	9	0	20	12	2	0	0	
13	1	0	18	56	0	22	4	2	0	0	0	0	1	0	0	0	0	0	0	2	6	0	2	4	0	0	0	
14	4	16	0	22	4	2	0	7	0	0	0	0	0	0	0	0	0	0	0	3	12	0	15	4	0	0	0	
15	0	13	0	24	3	3	1	0	0	0	0	0	0	7	0	0	0	0	0	2	14	0	15	9	2	0	0	
16	0	11	6	24	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	15	9	2	0	0	
17	3	8	8	21	9	8	3	0	0	1	0	0	0	0	0	0	0	0	0	1	11	0	6	0	0	0	0	
18	3	6	4	19	3	1	0	2	0	0	0	0	2	0	0	6	0	0	0	0	13	0	19	4	3	0	0	
19	9	2	19	13	3	0	3	0	0	1	0	0	0	0	0	0	0	0	0	7	18	0	12	11	2	0	0	
20	1	13	13	46	4	2	4	5	0	2	0	0	0	0	0	0	0	0	0	0	11	0	4	3	0	0	0	
21	2	4	5	14	5	3	0	3	0	0	1	0	0	2	0	1	0	0	0	1	31	0	4	3	0	0	0	
22	0	3	3	6	5	3	0	6	0	1	0	0	0	0	0	0	0	0	0	1	8	2	3	0	0	0	0	
	38	116	123	362	54	111	40	79	0	41	0	15	21	61	0	29	0	44	0	44	208	18	169	80	25	0	TOTAL	
	13	17	20	22	16	20	15	16	0	16	0	7	11	17	0	10	0	16	0	16	21	3	22	16	11	0	No. SESSIONS PERFORMED IN WHICH	
	59.1	72.3	90.9	100	72.7	90.9	68.2	72.7	0	72.7	0	31.8	50.0	77.3	0	45.5	0	72.7	0	72.7	95.5	13.6	100	72.7	50.0	0	% SESSIONS PERFORMED IN WHICH	
	40.53	118.76	20.39	13.55	20.39	13.55	13.55	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	20.30	161.42	29.61	29.61	29.61	29.61	29.61	29.61	CHL-SQUARE
	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	SIGNIFICANT P=0.05 []

Looking toward. Involves head turns, body turns, or other movements that result in a neighbor looking in the direction of the Wing-flagging male.

Vocalizing. Any call (e.g., long call) given by non-copulating birds.

Mounting. The male assuming a position on the female's back that is appropriate for Wing-flagging and copulation.

RESULTS

Description of Wing-flagging

The copulatory behavior of male Ring-billed Gulls includes a distinctive series of motor patterns apparently non-essential for fertilization. The performing male also utters a unique series of loud rhythmic notes resembling human laughter (*Ka-ka-ka-kakaka-kaka . . .*) during the latter part of the behavioral sequence. The frequency range and other characteristics of this prolonged call, hereafter referred to as the Copulation-call, are such that it is recognizable above the usual colony "noise." An observer located about 50 meters away can distinguish this call above other types being produced simultaneously by neighboring gulls. I am proposing that the conspicuous wing movements, which I have called Wing-flagging, combined with the distinctive Copulation-call and the exposed orange gape, further stimulate nearby gulls of both sexes to perform reproductive behavior and, because of these contagious effects, contribute to the synchronization of egg-laying and subsequently incubation for a large segment of the colony.

Precopulatory behavior may include courtship feeding of the female but more often it involves the female soliciting the male by facing him and slowly walking back and forth before him and head-tossing. The male may respond by walking round to the female's side, head-tossing, assuming an upright posture, and finally by mounting. Soft mewling notes are given by the female during certain periods of head-tossing. Occasionally, however, a male may mount a female without performing these preliminaries. On many occasions I have witnessed males mounting females that were settled on nests. In such instances, the females never responded sexually and usually remained in an incubating posture.

At the onset of copulatory behavior (Fig. 1a) the male mounts the female and stands in the middle of her back with his body essentially parallel to hers. The wings are partially extended and held above the horizontal and the beak is open. He then squats, fluffs his breast feathers, and raises the wings higher or extends them farther (Fig. 1b - h). A responsive female, usually one that was soliciting prior to mounting, head-tosses at this point and gently strokes the male's breast with her head. Occasionally she will bite at, or nibble, the male's breast feathers. This intensifies the male's activities and the wings are raised higher, rhythmically moved up and down in slow flaps, and the beak is opened wider exposing the bright orange mouth lining, and the Copulation-call is emitted (Fig. 1). Many mountings end at about this point but in the case of those culminating in successful matings the next step involves

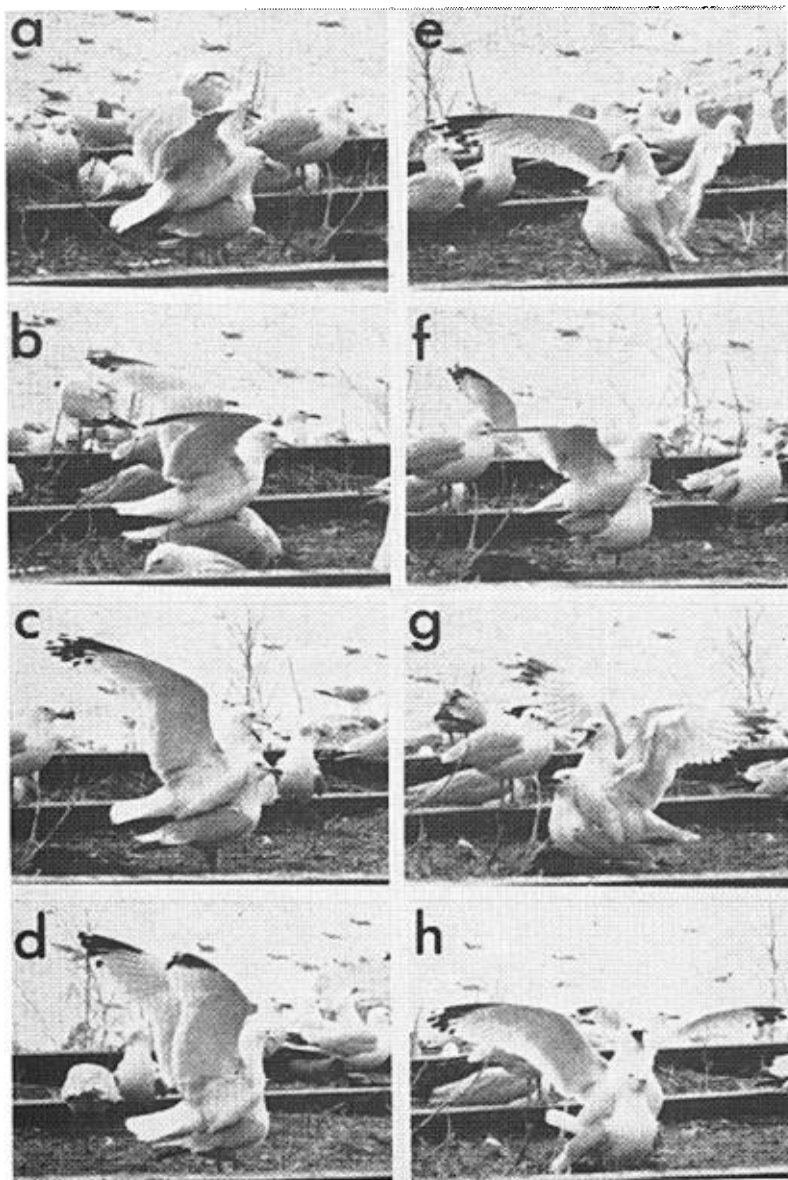


FIGURE 1a thru h. A series of postures assumed by a copulating pair of Ring-billed Gulls. Note the male's open mouth, the changing wing position, and the female's uplifted tail in photo h.

the female raising her tail and the male slipping his body to the side, wagging his tail back and forth and making cloacal contact. Wing-flagging movements and the rate of calling are intensified during the terminal stages.

Responses to Wing-flagging

Examination of the frequencies and totals for each of the 13 behavioral patterns for which I recorded data (Table 1) indicates that there are quantitative differences between the type of behavior that occurred during Wing-flagging and control periods.

Five of the 13 activities were performed exclusively by some of the controls, these being bill-pointing (72.7%), head-tucked (31.8%), nest building (45.5%), departures (72.7%), and arrivals (72.7%). However, as is indicated by the percentage figures parenthetically presented above, none of these were performed during all of the control periods (Table 1). These activities are suggestive of the typical daily activities that occur in the colony.

Five other activities (agonistic responses, walking toward, preening, soliciting, and plumage fluffing) were conducted at significantly higher rates ($P = 0.005$) during control periods. Although all of these activities were also performed during periods of Wing-flagging, the frequency of occurrence was much higher during control periods (Table 1). Thus, 10 of the 13 behavioral patterns I recorded were performed more often by control groups. The control periods were characterized by (1) more varied and higher rates of activity, (2) many birds being involved with comfort activities, (3) a significant amount of nest maintenance behavior, and (4) flight activity associated with feeding. Further support for my conclusion that higher rates of activity (as evidenced by the frequency of the 13 activities recorded) occur when Wing-flagging is not being performed, is provided by the fact that 11 of the 22 randomly paired observations (Table 1) had higher totals for the control periods than for periods of Wing-flagging. Ten of the 22 periods showed no significant difference between the two groups and one was higher during Wing-flagging.

Only one behavior was unique to periods of Wing-flagging, and this was mounting. During one-half of the copulations other males mounted females and began Wing-flagging. As many as four other males mounted during the short period of observation. However, the fact that the control periods were selected because copulation was not occurring at that particular time causes the total for this category to be of little significance. It is important to note, however, that during one-half of the filmed sequences 1 to 4 other males began copulating, possibly as a result of stimulation provided by the initial Wing-flagger. Occasionally these mountings took place in other than established territories (e. g., in a roadway adjacent to the colony). This observation substantiates Emlen and Miller's (1969) conclusion that pair ponds may be established prior to the establishment of territories. Other mountings occurred after the original performer dismounted but these were not included in my calculation.

Two of the 13 activities occurred at higher frequency during Wing-flagging; these were looking toward and vocalizing. Increased rates of both of these support the contention that neighboring birds are aware of Wing-flagging because of its signalling effect and that they respond to its occurrence. Often birds in nearby ter-

ritories gave long calls, made head thrusts at the mounted bird, and in other ways indicated direct stimulation.

These data support the contention that neighboring gulls are aware of Wing-flagging associated with copulation and that this produces an alternation in the ongoing behaviors, increases the tendency for physiologically-primed birds to perform sexual behavior. The combined effect is periodic spurts of copulatory behavior followed by lulls when tendencies for other activities predominate. Eventually a male mounts and the associated visual and auditory signals produce another series of matings. The contagiousness of the response usually peaks about the first of May when the appropriate endogenous state is probably likewise at its peak.

SUMMARY

The breeding cycles of many colonial species of birds is synchronized to some degree. Behavioral factors contribute to the pacing of the various events. The performance of courtship behavior by one pair can stimulate other pairs to perform the same behavior. In the case of Ring-billed Gulls and possibly other highly colonial Larids, a display associated with copulation, herein referred to as Wing-flagging, produces a significant shift in ongoing activity and increases the likelihood that other pairs will copulate. A comparison of behavior observed during 22 control periods (i. e., without copulation) with that recorded during 22 periods when copulation was occurring indicate significant differences in the frequencies of 13 activities selected as indicators.

Wing-flagging is described and its relation to the breeding itinerary is discussed. The obvious ritualized wing movements during copulation and a unique Copulation-call that is given while the bright orange gape is exposed function as a signal that assists in synchronizing stages in the breeding cycle. In spite of the tendency toward synchronized breeding by Ring-billed Gulls, a significant number of pairs will nest slightly later. In most instances these birds were probably late arrivals at the colony.

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