

DAILY ACTIVITY PATTERNS OF BREEDING RING-BILLED AND CALIFORNIA GULLS

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The daily activity patterns of gulls have been studied to the extent that some generalities have been made. For example, the number of gulls present at a breeding colony varies with the tidal cycle in Herring Gulls (*Larus argentatus*; Drent 1967, Galusha and Amlander 1978) and with the time of day in Black-headed (*Larus ridibundus*; Patterson 1965), Lesser Black-backed (*Larus fuscus*; Delius 1970) and Laughing gulls (*Larus atricilla*; Burger 1976). Moreover, there is some indication that activity of gulls at the breeding colonies may not be randomly distributed in time. Delius (1970) reported a diurnal cycle in the percentage of Lesser Black-backed Gulls sleeping and engaging in other activities but not in the percentage of birds preening. Galusha and Amlander (1978) found that the number of sleeping Herring Gulls peaked during midday and again at around midnight, while the number of gulls at rest varied inversely. Burger (1976) found that Laughing Gulls exhibited a diurnal pattern in their territorial defense, courtship, and copulatory activity. Unfortunately, most of these studies grouped behavioral patterns into broad categories rather than examining each specific pattern separately. Because of this, it is difficult to determine how frequencies of individual behavioral patterns change during the course of the day or how the activity patterns of related behaviors vary from each other. The objective of our study was to ascertain the frequency of specific behavioral patterns in California (*Larus californicus*) and Ring-billed gulls (*L. delawarensis*) and to compare the daily activity patterns of these species when breeding in the same colony.

One of the more important discoveries of ethology has been that the specific form of a certain behavioral pattern often varies among related species. Possibly behavioral patterns also differ among related species in their frequency of occurrence. This, however, has not been adequately documented primarily because of the difficulty of studying different species under identical climatic and environmental conditions. We minimized this difficulty by studying California and Ring-billed gulls because in some colonies they not only nest together but often locate their nests side by side.

METHODS

Observations were made on a colony of Ring-billed Gulls nesting on an island in Sprague Lake, Washington (Conover et al. 1979) during March-July 1977 and 1978. The 400 to 500 California Gulls which nested together with the 1700 Ring-billed Gulls were observed in 1978. Observations were made 100 m from the colony, using a 15-45× spotting scope. Usually the gulls were observed all day for one or two days a week.

Data for this study were gathered by watching gulls in three sampling

areas located inside the colony. Each area was approximately 10 m in diameter. Within these areas, approximately 130 pairs of Ring-billed Gulls and 20 pairs of California Gulls nested both in 1977 and 1978. Daily patterns in the number of gulls present at the colony were determined by hourly counts of gulls inhabiting the sampling areas. Activity patterns were measured by randomly selecting a gull from within one of the sampling areas and recording its behavior after a 30-sec delay. Gulls were selected by randomly choosing one of 30 numbered markers that had been placed in the study areas prior to the gulls' breeding season and observing either the Ring-billed or California gull closest to that marker. During 1978, observations on Ring-billed and California gulls were alternated so that both species were equally observed. Usually 70 to 100 records were obtained hourly, providing a sample large enough to permit analysis of infrequent behavioral patterns. The following patterns were recorded: standing, sitting, or walking in either an alert (neck outstretched) or relaxed position; sleeping (head tucked under the wing); preening; long calling; giving a single call note ("keew" calling); engaging in agonistic behaviors; upright displaying; choking displaying; copulating; or nest making (gathering or arranging nesting material). Most of these action patterns have been described by Tinbergen (1953, 1959) and Moynihan (1958a, 1958b). The duration of 60 complete copulations (cloacal contact) was also measured for each species by recording the time one gull was mounted on the other.

The percent of time each species spent in a particular behavior was determined for each hour of observation in the following manner: the number of times a gull was observed engaging in a certain behavior was divided by the total number of observations made that hour. A record was made of which species spent more time engaged in a particular behavior during each hour of observation. Hourly results from the entire breeding season were then analyzed by the sign test to find out whether the species differed significantly in the amount of time they spent engaged in a particular behavioral pattern. Data from the pre-incubation period (prior to 15 May when half of the clutches of both the Ring-billed and California gull were completed) were analyzed separately from data of the incubation—post-hatch period (after 15 May).

Daily patterns of activity were compared for a 4-hour morning period (06:00 to 10:00 Pacific Standard Time) and a 4-hour late afternoon period (16:00 to 20:00) to a 4-hour midday period (11:00 to 15:00) by using the median test.

RESULTS

Daily population pattern.—During the pre-incubation period, the number of Ring-billed and California gulls occupying the three sampling areas varied greatly during the day (Figs. 1 and 2). Both populations peaked in the early morning and then declined; by midday the number of both Ring-billed ($\chi^2 = 83.42$, $P < 0.001$) and California gulls ($\chi^2 = 8.24$, $P < 0.01$) had declined. In the afternoon, the number of both

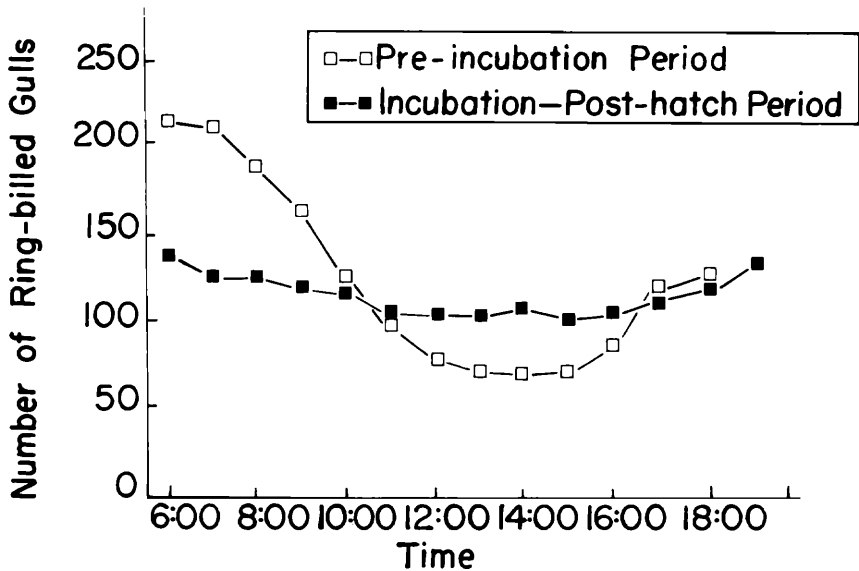


FIG. 1. The number of Ring-billed Gulls in the sampling areas at different times of the day during the pre-incubation and incubation-post-hatch periods.

species present in the sampling areas increased so that the number of Ring-billed ($\chi^2 = 13.00$, $P < 0.001$) and California gulls ($\chi^2 = 4.5$, $P < 0.05$) was significantly higher in the late afternoon period than in the midday period.

During the incubation and post-hatch period, the populations of both Ring-billed and California gulls continued to exhibit the same diurnal pattern as during the pre-incubation period, but the population fluctuations were less pronounced. Still, the number of Ring-billed Gulls was significantly lower during the midday than in the morning ($\chi^2 = 10.90$, $P < 0.001$) or late afternoon periods ($\chi^2 = 12.96$, $P < 0.001$). The midday California Gull population was significantly lower than its late afternoon population ($\chi^2 = 7.2$, $P < 0.01$) but not from its morning population ($\chi^2 = 0.25$).

Daily activity patterns.—The frequency of many behavioral patterns, as well as the copulation duration, did not vary significantly during the different periods of the day for either species (Tables 1 and 2). When data for the entire reproductive season were analyzed, Ring-billed Gulls spent significantly less time in the morning sitting relaxed than during the midday period, and more time walking, long calling, and engaging in territorial behavior (agonistic behavior, upright display, and oblique-forward display). These differences are especially pronounced during the pre-incubation part of the breeding season (Table 1). Ring-billed Gulls also spent significantly less time in the late afternoon period in an

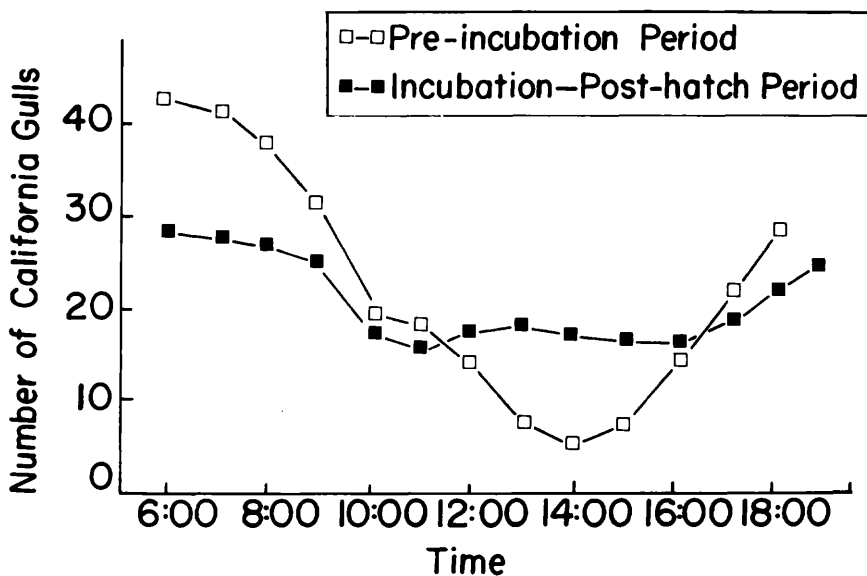


FIG. 2. The number of California Gulls in the sampling areas at different times of the day during the pre-incubation and incubation-post-hatch periods.

upright display than during the midday, and more time standing, preening, and giving the choking display.

California Gulls showed fewer significant differences than Ring-billed Gulls in their daily activity patterns owing, in part, to greater daily variation in activity patterns. When data for the entire reproductive season were combined, California Gulls exhibited a significant increase in the time spent sitting relaxed and a decrease in the choking display from the morning to the midday periods.

Interspecific differences in activity patterns.—The frequency of several behavioral patterns differed between Ring-billed and California gulls (Table 3). During the pre-incubation period, California Gulls spent significantly more time preening than did the Ring-billed Gull, whereas the latter spent more time in an alert position, upright display, oblique-forward display, long calling, “keew” calling, and engaging in agonistic behaviors. Also, the duration of copulations was almost twice as long in California as in the Ring-billed gulls. During the incubation-post-hatch period, California Gulls spent significantly more time than Ring-billed Gulls in sleeping and preening, but less time in an oblique-forward display, long calling, engaging in agonistic behaviors, and in gathering and arranging nest materials. When data for the entire reproductive season were combined, California Gulls again spent significantly more time sleeping and preening, while Ring-billed Gulls spent significantly more time in an alert position, upright display, oblique-forward display,

TABLE 1.

Mean percent of time spent in various activities by Ring-billed Gulls at different times of the day. (Asterisks between morning and midday values or between midday and afternoon values indicate that those values are significantly different.)

	Pre-incubation			Incubation—post-hatch			χ^2 for combined data	
	Morning	Midday	After-noon	Morning	Midday	After-noon	Morning vs. midday	Midday vs. evening
Maintenance behaviors								
Standing relaxed	40.8	43.8 *	44.8 *	46.9 **	34.1	47.3	0.0	4.06*
Sitting relaxed	11.4 *	17.6 *	19.3 *	22.7 *	27.2	18.2	8.79**	3.40
Walking relaxed	4.0 *	3.9	3.0	2.4	2.0	2.1	5.21*	0.11
Sleeping	6.5	5.8	4.9	6.9 *	18.3 *	11.9	0.19	4.23*
Preening	10.1	8.5 **	10.3 **	9.2	10.8 *	12.4 *	0.13	12.54***
Wariness								
Alert postures	9.8	7.3	6.4	3.3	2.1	1.8	0.72	0.69
Vocal behaviors								
Long calling	3.0 *	1.5	1.5	2.0	1.3	1.8	7.08**	1.23
<i>Keew</i> calling	0.4	0.5	0.2	1.6	0.2	0.1	0.52	0.40
Territorial behaviors								
Agonistic behaviors	2.2 *	1.0	1.6	1.6	1.5	1.1	4.40*	0.00
Upright display	6.6 *	5.0 *	3.3	1.5	1.1	1.1	4.46*	6.23*
Oblique-forward display	1.6 *	0.9	0.6	0.5	0.3	0.7	4.28*	0.03
Courtship/reproductive behaviors								
Copulating	0.6	0.5	0.8	0.0	0.0	0.0	1.90	0.97
Head tossing	2.0	2.2	2.6	0.5	0.1	0.2	1.60	0.04
Nest making	0.4	0.6	0.6	0.8	0.5	0.3	1.07	0.20
Choking display	0.5	0.2 *	0.8	0.2	0.0	0.1	6.54*	4.35*
Copulation duration (sec)	48.4	59.0	50.0				0.04	0.01

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

TABLE 2.
Mean percent of time spent in various activities by California Gulls at different times of the day. (Asterisks between morning and midday values or between midday and afternoon values indicate that those values are significantly different.)

	Pre-incubation			Incubation—post-hatch			χ^2 for combined data	
	Morning	Midday	Afternoon	Morning	Midday	Afternoon	Morning vs. midday	Midday vs. afternoon
Maintenance behavior								
Standing relaxed	38.5	32.3	41.3	42.5	50.9	37.9	0.06	1.85
Sitting relaxed	2.1	13.3	11.7	25.2	12.6	18.0	4.04*	0.01
Walking relaxed	4.1	2.3	6.7	1.3	2.4	6.1	0.24	2.81
Sleeping	18.1	8.9	11.7	10.1	9.9	10.1	0.18	0.48
Preening	19.2	29.2	14.0	15.0	16.8	**	2.08	1.23
Wariness								
Alert postures	7.9	4.1	5.5	2.8	2.4	1.7	0.04	0.00
Vocal behaviors								
Long calling	0.3	0.2	1.0	0.3	1.2	0.3	0.19	0.10
Keew calling	0.4	0.0	0.2	0.2	1.2	0.0	0.00	0.00
Territorial behaviors								
Agonistic behaviors	1.7	0.4	2.0	0.8	0.8	0.4	0.24	0.00
Upright display	0.5	3.0	0.7	0.0	0.3	0.0	0.01	0.36
Oblique-forward display	0.2	0.0	0.6	0.0	0.0	0.0	0.60	0.54
Courtship/reproductive behaviors								
Copulating	0.6	1.1	0.0	0.0	0.0	0.0	0.04	0.10
Head tossing	1.7	2.6	2.6	0.0	0.0	0.0	0.19	0.00
Nest making	0.2	1.0	1.2	0.0	0.5	0.0	0.19	0.23
Choking display	1.6	0.0	0.3	0.0	0.0	0.0	5.48*	1.18
Copulation duration (sec)	100.7	80.0	83.0				1.21	0.25

* $P < 0.05$ ** $P < 0.01$

TABLE 3.

Mean percent of time spent in various activities during the pre-incubation and the incubation-post-hatch periods by California and Ring-billed gulls and the results of sign tests comparing the activity patterns of the two species for significant differences.

	Pre-incubation			Incubation-post-hatch			Com- bined data
	Ring- billed Gull	Cali- fornia Gull	Z	Ring- billed Gull	Cali- fornia Gull	Z	Z
Maintenance behaviors							
Standing relaxed	40.7	37.2	0.29	41.9	38.0	1.22	1.29
Sitting relaxed	3.1	8.1	1.38	28.1	22.2	1.70	0.11
Walking relaxed	3.8	4.5	1.11	2.1	2.4	0.21	0.76
Sleeping	8.1	12.8	1.53	8.3	12.9	3.08**	3.33***
Preening	9.8	21.2	4.68***	10.1	19.5	3.86***	6.15***
Wariness							
Alert postures	11.1	6.2	3.39***	2.4	1.5	0.00	2.54*
Vocal behaviors							
Long calling	2.4	0.4	3.95***	1.6	0.4	2.59**	4.86***
<i>Keew</i> calling	0.7	0.2	1.98*	0.5	0.7	0.27	1.54
Territorial behaviors							
Agonistic behaviors	1.8	1.2	1.98*	0.9	0.2	2.65**	3.25**
Upright display	7.5	1.5	4.63***	1.1	0.2	1.58	4.98***
Oblique-forward display	0.7	0.4	2.44*	0.5	0.0	2.27*	3.46***
Courtship/reproductive behaviors							
Copulating	0.4	0.8	1.25	0.0	0.0	0.00	1.25
Head tossing	1.9	2.3	0.00	0.3	0.1	0.89	0.51
Nest making	0.4	0.5	0.55	0.5	0.2	2.02*	2.00*
Choking display	0.4	0.7	0.80	0.0	0.0	0.00	0.80
Copulation duration (sec)							
	50.1	91.6	$\chi^2 = 11.2***$				

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

long calling, engaging in agonistic behaviors, and in gathering and arranging nest materials.

DISCUSSION

Variation in numbers and activity during the day.—In the first part of the breeding season, the numbers of Ring-billed and California gulls occupying the colony site varied greatly during the day. Throughout the incubation-post-hatch period, this same pattern was evident but less pronounced. One reason for the smaller fluctuation in the number of gulls during the latter period is because one gull must always be present

at each nest during this period to incubate and protect the eggs and chicks from neighboring gulls. Also once the chicks hatch, their food requirements often require the other parent to search for food, making it harder for both parents to be at the nest simultaneously.

The pattern of both the Ring-billed and California gull populations peaking in the early morning and again towards evening is similar to that observed in Laughing (Burger 1976) and Black-headed gulls (Patterson 1965). Galusha and Amlander (1978) and Delius (1970), however, found no daily pattern in the number of Herring and Lesser Black-backed gulls at the colony, respectively.

In studying the Laughing Gulls, Burger (1976) found that courtship and territorial activities peaked in early morning and late afternoon, with little or no activity during midday. For most of its behavior, the California Gull failed to show a midday lull or any other diurnal change in activity; rather it showed a fairly constant rate of behavior throughout the day. The California Gull exhibited no significant difference among any of the three time periods in its territorial or courtship behavior, nor did any of these related behavioral patterns fluctuate as a group, although there was occasionally a significant difference between time periods in the frequency of some maintenance behavior.

The daily activity pattern of Ring-billed Gulls appeared to differ from both the California Gulls observed in this study and the Laughing Gulls observed by Burger (1976). The Ring-billed Gull spent more time in territorial behavior during the morning than during any other time of the day, especially in the pre-incubation period when the gulls are first establishing their territories. This high level of territorial defense in the morning may also explain why long calling and walking were also more frequent in the morning. Long calling is often used in territorial defense as a threat behavior and territorial disputes require the gulls to increase their walking since they have to move from one part of their territory to another. Unlike the Laughing Gull, however, the Ring-billed Gull did not exhibit an increase in territorial behavior again in the afternoon and did not show any consistent daily pattern in its courtship and reproductive behavior.

There were other differences between the daily activity patterns of Ring-billed and California gulls and those of other gulls. Burger (1976) showed that in Laughing Gulls the copulations occurring in the morning and late afternoon were significantly longer than those at midday. No significant difference in duration of copulation was observed in our study between the morning and midday periods or between the midday and late afternoon periods. Both Lesser Black-backed (Delius 1970) and Herring gulls (Galusha and Amlander 1978) sleep more at midday than during the rest of the day. This same pattern was shown in our study by Ring-billed Gulls during the incubation-post-hatch period but not during the pre-incubation period. In contrast to other gulls, the California Gull slept less during the midday than during either the morning or later afternoon period throughout both reproductive periods.

The large midday decline in the numbers of both Ring-billed and California gulls, especially during the pre-incubation period, and the absence of more pronounced diurnal variation in activity patterns, perhaps relate to the gulls' wariness while on the colony site (where they are susceptible to ground predators). Individuals may spend most of their loafing and other free time in a safer location, while staying in the colony only long enough to establish and maintain a territory, attract a mate, and to protect eggs or chicks. In fact, during the midday, many gulls could be observed sitting out in the water several hundred meters from the island, particularly during the pre-incubation period. If these gulls had chosen instead to loaf at the colony site, the variation in daily activity patterns would have been more pronounced and perhaps more similar to the Laughing Gull which apparently does loaf at the colony site.

Interspecific differences in activity patterns.—Almost all gull species exhibit the same array of reproductive behavior patterns, although the specific form of these patterns often varies among species. Furthermore, the results of this study indicate that the frequency of these behavioral patterns can also vary among gull species even when the different species are nesting in the same colony and encountering similar climatic and environmental conditions. Our observations indicate that California Gulls spent more time sleeping and preening than Ring-billed Gulls while the latter spent more time in an alert position, long calling, and in all territorial behaviors. These differences may be associated with the closer nest spacing of the Ring-billed Gulls in their smaller territories. At the Sprague Lake colony where this study was conducted, the mean distance between the nest of a Ring-billed or California gull and the nearest neighboring nest was 0.6 and 2.4 m, respectively. The closer spacing of Ring-billed Gulls may account for their more frequent alert postures, agonistic interactions, and threat displays because they must maintain more rigid territorial boundaries; otherwise their eggs and chicks would be easy prey to neighboring gulls. In the same light, their much shorter duration of copulation may be an evolutionary result of more frequent interference from nearby gulls; for indeed, we often observed copulation attempts by Ring-billed Gulls being interrupted by neighbors.

In contrast, the California Gulls, slightly larger, more dominant and more widely spaced in larger territories, may be generally more tolerant of neighbors while maintaining more elastic territorial boundaries and responding less vigorously to intruders as long as they do not come near the nest site. Both Ring-billed and California gulls breed on inland islands where they may be more susceptible to predators than coastal-nesting gulls because the latter's colonies are often more difficult for predators to reach (Conover and Miller 1978). The smaller territories of Ring-billed and California gulls may be an evolutionary response to higher predation pressure. The closer spacing should result in more gulls being available to mob or swoop at a predator, thus making such

tactics more effective. In addition, simply being near many other gulls reduces an individual's chance of capture by a predator (Hamilton 1971). There are, however, certain liabilities associated with dense nesting that counterbalance the advantages. Disadvantages include the increased susceptibility of the eggs and chicks to cannabilistic gulls which can more easily traverse the shorter distance between the territorial boundaries and the nest before the parents can respond; the increased danger of chicks straying into other gulls' territories and being attacked (Conover et al. 1980); and as the results of this study suggest, more time and energy must be devoted to territorial defense, leaving less for other necessary activities.

SUMMARY

The number of both California and Ring-billed gulls present at the colony peaked in the early morning and late afternoon during both the pre-incubation and incubation-post-hatch periods. This pattern was not as pronounced in the latter period. Ring-billed Gulls engaged in more territorial behavior in the morning than at other times of the day. However, they did not significantly alter the frequency of their courtship-reproductive or maintenance behavior during the day.

By contrast California Gulls showed a fairly constant rate of behavior throughout the day. These gull species also differed from each other in distribution of their time among different behavioral patterns. Ring-billed Gulls spent significantly more time than California Gulls in an alert position, long calling, engaging in territorial behavior (agonistic behavior, upright display, oblique-forward display), and in gathering and arranging nesting materials. California Gulls spent more time sleeping and preening. These differences may be associated with the closer nest spacing of the Ring-billed Gull.

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