DAILY AND SEASONAL ACTIVITY PATTERNS IN BREEDING LAUGHING GULLS

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THE presence of daily and seasonal activity patterns in birds is established in the minds of many field researchers (Craig 1918, Marler and Hamilton 1967). Apart from references to birds singing less frequently in the middle of the day than in the early morning and late afternoon (Van Tyne and Berger 1959, Berger 1961, Nice 1937, Robbins and van Velzen 1970), few quantitative studies of the daily activity patterns in wild birds have been made. Cullen (1954) and Karplus (1952) studied the diurnal activity rhythms of birds in the arctic summer. Müller-Schwarze (1968) studied the circadian rhythms of the Adélie Penguin (*Pygoscelis adeliae*) during the austral summer and concluded that a midday minimum is common to all forms of activity, with activity maxima in the morning and evening.

A number of laboratory experiments show a circadian pattern in the onset and cessation of activity (Farner and Mewaldt 1953, Aschoff 1965, Farner 1965, Smith et al. 1969.) These authors were interested in the role of photoperiodism in regulating the onset of activity, and paid little attention to the type, quality, or quantity of that activity. Eyster (1954) examined captive songbirds for patterns in song activity, and Morton (1967) studied feeding rhythms of White-Crowned Sparrows (*Zonotrichia leucophrys gambelii*) under field and laboratory conditions. Other laboratory studies have concentrated on the implications of circadian rhythms and photoperiodic regulation in the annual reproductive cycle of birds (Wolfson 1965, Heppner and Farner 1971).

I studied Laughing Gulls (*Larus atricilla*) in Brigantine, New Jersey to determine daily and seasonal rhythms of activity during the 14-day period prior to egg-laying, and during the 14-day period after egg-laying. I wanted to determine if activity patterns changed as a result of the constraints of courtship and incubation. I also examined the data for qualitative as well as quantitative changes in the behavior.

MATERIALS AND METHODS

I conducted fieldwork during May and June 1973 in the gullery on Brigantine National Wildlife Refuge, New Jersey. The colony is in a *Spartina alterniflora* salt marsh divided into islands by a series of tidal creeks. At high tide low parts of the marsh are inundated, and at low tide some of the creeks are almost empty.

The colony was spread over the marsh and was denser in some places than others. I selected two parts of the marsh for this work. Study area 1, next to Clark Creek, was 100 m long by 100 m wide and contained many small pools and *Spartina* mats. These mats are dead grass from the previous year, left there by high tide action. Area 1 was used for study during the courtship phase prior to egg-laying. Later in the season this part of the marsh contained 78 nests. Study area 2, near the end of Mile Creek, was 8 m wide and 30 m long. It contained 20 nests and was used during the incubation period only.

I studied the activity patterns of pre-egg laying Laughing Gulls in study area 1 for 14 days before the first eggs were laid. For this purpose I entered the blind daily at approximately 0600 and remained until 2100. I recorded two types of data during this period. First, during a 5-min sample period each half hour, I counted the number of gulls preening, bathing, swimming, feeding, courting, fighting, resting, and flying. Secondly, I recorded the number of copulations occurring each hour, and the duration of each complete copulation seen.

In the 14-day period after egg-laying I studied 20 color-marked pairs in study area 2. Egg-laying was completed in all 20 nests prior to initiation of my work. I watched from a blind during the same time periods as in the pre-egg phase. During the 5-min sample periods each half hour, I recorded the number of birds incubating and the number of nests with both members of the pair present. The total number of birds adding nest material, giving intruder displays, and copulating was recorded for each hour.

Data from the pre-egg and incubation periods were analyzed for daily and seasonal variations in various activities. The results for each activity are first organized for an examination of daily patterns, and then for an examination of seasonal patterns. Results are given as the percentage of birds present engaging in each activity unless specified otherwise.

Results

Pre-egg Phase

Laughing Gulls arrive on the colony in mid- to late April when the marsh is still covered with dead *S. alterniflora* from the previous year. By early May, the marsh contains courting groups and pairs on territory. Courting groups are more often on the *Spartina* mats, whereas pairs are usually in the growing *Spartina*. Members of an established pair often remain on their territory for much of the day. They defend the territory by chasing and attacking intruders that land within 5 m. Courting birds often display on several different mats scattered over the marsh. Some individuals, recognizable by oil marks or plumage patterns, return to the same mat sporadically during the pre-egg period.

Number of birds on the study area.—The number of birds present in the study area was recorded in 5-min sample periods every half hour during the day. Two peaks in activity occurred at 0730 and 1930, with the least number of birds present at 1130 (Fig. 1). An ANOVA followed by an F test for significance indicates that the morning peak and the noon low are significantly different ($F = 23.54$, $N = 24$, $P < 0.001$), the evening peak and the noon low are significantly different ($F = 32.09$,

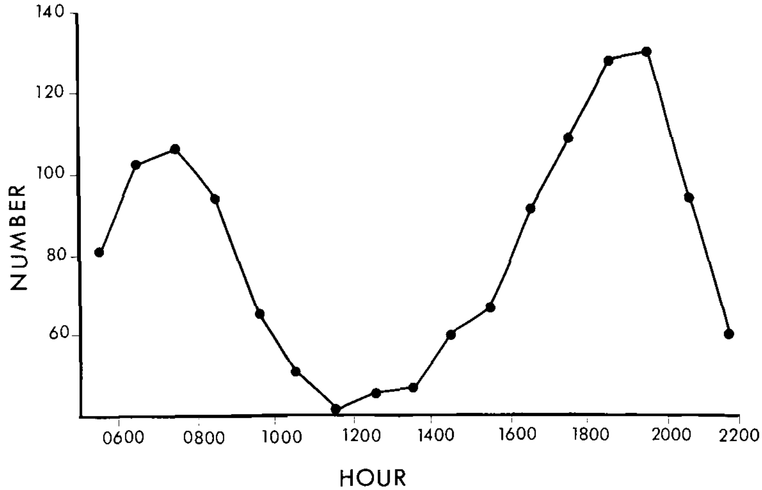

Fig. 1. Number of birds on the study area as a function of the hour of the day. Data from the 14-day period prior to egg-laying.

N = 24, $P < 0.001$), and the peaks are not significantly different from one another ($F = 1.96$, N = 24).

The range and standard deviations for these data are large (Table 1) because the data are lumped over the 14-day period. Examining the data for changes during the 14-day period indicates a nonsignificant correlation between date and number of birds present at 0730 (r = 0.31, df =

TABLE 1
NUMBER OF BIRDS ON THE STUDY AREA AS A FUNCTION OF THE TIME OF DAY

Hour	Mean	+ SD	Range
0500–0600	80	20	62–93
0600–0700	102	18	76–117
0700–0800	106	30	56–128
0800–0900	96	33	63–132
0900-1000	65	30	48–84
1000–1100	51	27	12–72
1100–1200	41	24	22–78
1200–1300	46	17	21–78
1300–1400	47	21	32–85
1400–1500	61	21	33–75
1500–1600	68	28	36–138
1600–1700	89	34	36–129
1700–1800	108	38	38–155
1800–1900	127	40	66–191
1900–2000	128	42	69–187
2000–2100	92	41	40–179
2100–2200	62	18	21–73

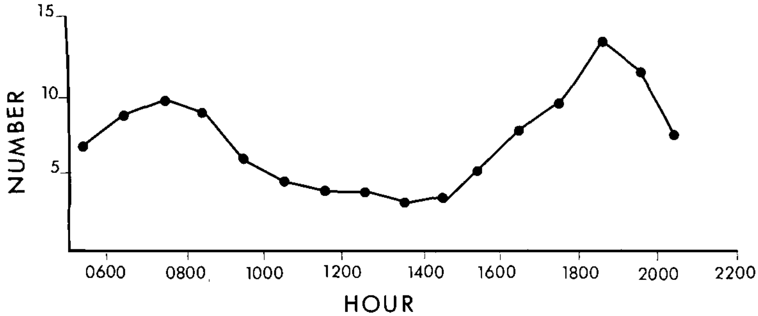

Fig. 2. Mean number of pairs (out of 20) courting as a function of the hour of the day. Data are summed for the 14-day pre-egg period.

10), and a significant correlation in the number of birds present at 1130 ($r = 0.58$, df = 10, $P < 0.05$) and at 0730 ($r = 0.71$, df = 10, $P < 0.005$).

In summary, the number of birds active on the study area was significantly higher in the early morning and late afternoon than at midday, and increased from day to day as laying approached.

Courtship activity.—Courtship activity in unmated birds consists of directing long calls, head tosses, and croons at potential mates flying overhead. If the potential mate lands, courtship begins. Courtship sequences on the ground include long calls, croons, head tosses, facing away, running or walking away, courtship feeding, and copulation. Noble and Wurm (1943) described courtship in Laughing Gulls. As pair bonding proceeds, the pair often moves off the mat to the fresh *Spartina*. Pairs defending territories (i.e. chasing and attacking intruders) continue to court and copulate until egg-laying.

Courtship activity showed peaks at 0730 and 1830, with a low at 1330. The peak at 0730 is significantly higher than the low at 1330 ($F = 22.64$, df = 22, $P < 0.001$), the high at 1830 is significantly different from the low at 1330 ($F = 25.87$, df = 22, $P < 0.001$), but the peaks are not significantly different from one another ($F = 2.1$, df = 22). A courtship activity frequency curve is shown for the 20 pairs of gulls nearest the blind (Fig. 2).

Copulation activity.—The first copulation occurred on 9 May, and it increased in frequency thereafter. Individual pairs were seen copulating as often as nine times in one day. The mounting male wingflaps while giving a copulatory call, and the white wings flashing can be seen far across the marsh.

The number of copulations was recorded continuously during the pre-

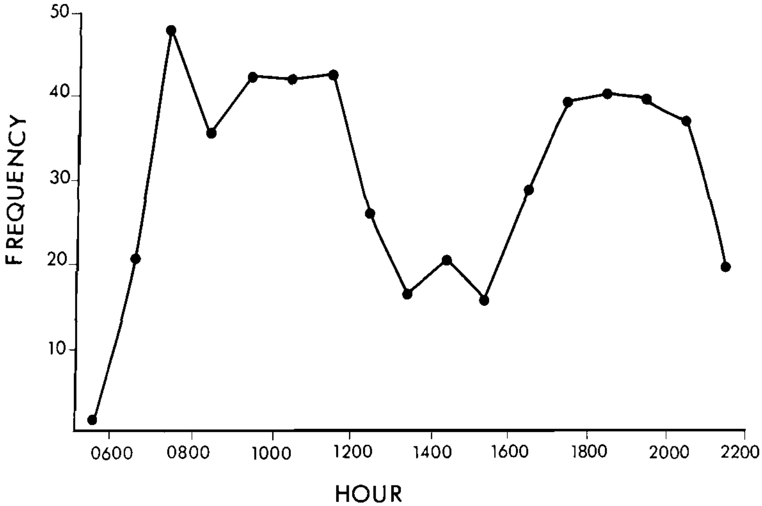

Fig. 3. Frequency of birds engaged in copulation as a function of the hour of the day. Frequency refers to the percentage of birds engaged in the activity.

egg phase. The mean copulation frequency (number of copulations per hour) varied with peaks at 0730 and 1830, with a low copulation frequency at 1330 m (Fig. 3). An ANOVA and F test for significance indicates that the high frequency at 0730 is significantly different from the low at 1330 ($F = 12.1$, df $= 20$, $P < 0.01$), the high frequency at 1830 is significantly different from the low at 1330 ($F = 10.9$, df $= 20$, $P < 0.001$), and the two high frequencies are not significantly different from one another ($F = 0.10$, df$=20$).

The durations of copulations were timed as often as possible during each hourly period for the 14-day pre-egg phase. The copulation duration is defined as the mount time as evidenced by the characteristic wing-flapping of the male. The mean copulation duration varied with the longest copulations coincident with the daily peaks in copulation frequency. Short copulation durations were recorded at 1230 (Fig. 4). The mean duration time for the peak at 0730 is significantly different from the low at 1230 ($F = 10.1$, df $= 66$, $P < 0.01$), the peak at 1830 is significantly different from the noon low ($F = 12.2$, df $= 89$, $P < 0.01$), and the two peaks are not significantly different from each other ($F = 0.55$, df $= 95$).

The pattern of short copulations in the very early morning, longer copulations in early morning, short copulations in the middle of the day,

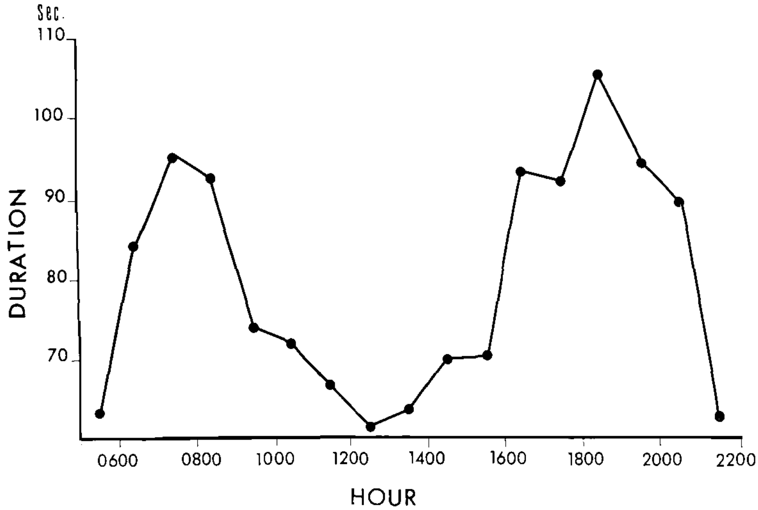

Fig. 4. Mean duration of copulation as a function of the hour of the day. Data summed for the 14-day period prior to egg-laying.

TABLE 2
DURATION OF COPULATIONS AS A FUNCTION OF TIME FOR INDIVIDUAL PAIRS OF LAUGHING GULLS[1]

Individual	Time	Duration (sec)
A	0655	110
	0657	135
	0710	165
	0745	100
	0840	48
	1210	32
	1610	110
	1815	155
B	0715	60
	0812	80
	0825	65
	0847	65
	0936	40
	0952	38
	1150	65
	1725	112
	1745	152
C	0812	65
	0820	115
	0825	65
	0925	80
	0955	15
	1610	97
	1655	125

[1] Data from 22 May 1973.

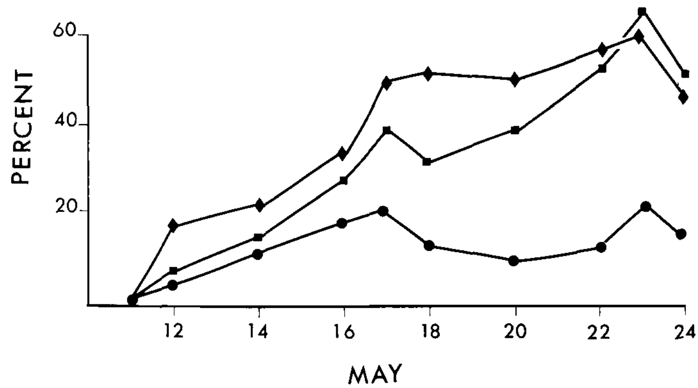

Fig. 5. Percent of birds engaged in copulation as a function of date. The diamond line represents data collected at 1800–1900, the square line at 0700–0800, and the circle line at 1300–1400.

and longer copulations in late afternoon was also typical of individual pairs (sample shown in Table 2).

Examining the copulation frequency data for seasonal differences indicates an increase in frequency with time (Fig. 5). Frequency of copulation and date for the samples at 0730 are highly correlated (r = 0.86, df = 8, $P < 0.01$), 1330 (r = 0.94, df = 9, $P < 0.005$) and 1830 m (r = 0.92, df = 8, $P < 0.005$).

The mean duration of copulation also increased during the 14-day period (Fig. 6). The correlation of mean copulation duration with date is significant at the 0730 peak (r = 0.89, df = 8, $P < 0.001$), the 1230 low (r = 0.95, df = 8, $P < 0.001$) and the 1830 peak (r = 0.81, df = 9, $P < 0.01$).

Territorial defense.—Laughing Gulls defend their territories in the pre-egg phase by chasing intruders and by attacking them. Individual fighting sequences often are as long as 10 min, with pecking, wingpulling, wingflapping, and billpulling. The percentage of gulls engaged in territorial defense was relatively small at any one point in time. Therefore, I have analyzed the data for peak and low periods of activity only. Peak activity was from 0600–0700 and from 1600–1900, with low activity from 1100–1400. A Student's *t*-test indicates that the peak period of fighting at 0600–0900 is significantly different from the low at 1100–1400 ($t = 2.1$, df = 51, $P < 0.01$), the peak from 1600–1900 is significantly different from the low at 1100–1400 ($t = 3.34$, df = 51, $P < 0.005$), and the peaks are not significantly different from one another ($t = 1.1$, df = 51).

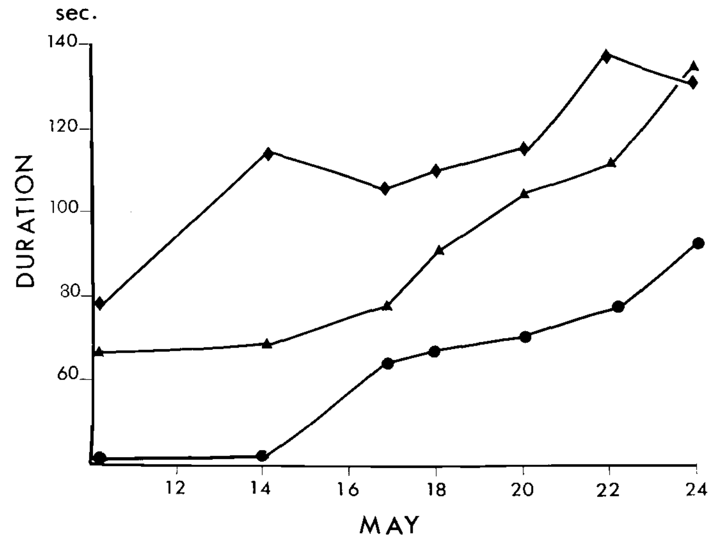

Fig. 6. Duration of copulation as a function of date. The diamond line represents 1800–1900, the triangle line is 0700–0800, and the circle line is 1300–1400.

The level of overt attack was so low during the period that I did not analyze the seasonal activity by time periods. Instead, fighting was summed for each day and correlated with the date (Table 3). Fighting increased significantly during the pre-egg period ($r = 0.90$, df $= 12$, $P < 0.005$).

Daily patterns of other activities.—The number of birds engaging in activities other than courtship and territorial defense was relatively small during the 14-day period, but the activity patterns followed closely the pattern for the number of birds present on the study area.

Seasonal patterns of other activities.—The data for every 5-min sam-

TABLE 3
Gull Activities as a Function of Date during the Pre-egg Period

Activity	r	Significance
Resting	− 0.70	$P < 0.01$
Preening	− 0.41	NS[1]
Courting	+ 0.82	$P < 0.005$
Feeding	0.00	NS
Fighting	+ 0.90	$P < 0.005$
Flying	− 0.10	NS
Bathing	− 0.29	NS
Swimming	+ 0.47	NS

[1] NS = not significant.

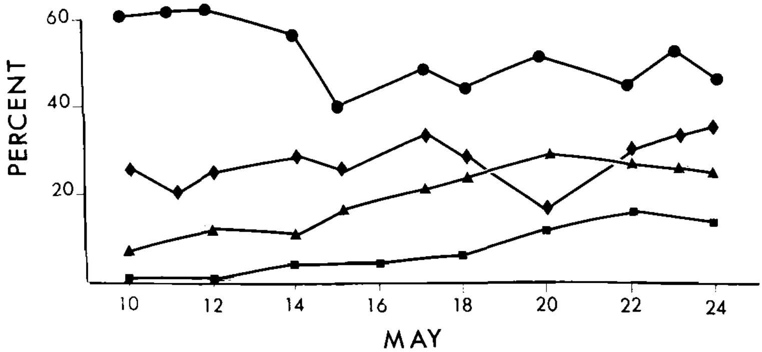

Fig. 7. Percentage of gulls engaged in various activities as a function of date. The circle line is resting, the diamond line is flying, the triangle line is courting, and the square line is fighting.

ple period were summed daily for each activity to determine seasonal patterns. The correlations between date and the percentage of birds engaged in various activities are given in Table 3, and selected patterns are plotted in Fig. 7. Only those activities concerned with courtship and territorial defense increased during the 14-day period. Maintenance activities (bathing, swimming, preening), flying, and feeding activities remained relatively constant during the period. The percentage of birds resting on the study area decreased significantly over the 14-day pre-egg period ($r = -0.7$, df $= 12$, $P < 0.01$).

Tidal pattern of feeding activity.—Most of the Laughing Gull's daily feeding activities occurred outside the study area, though a few gulls did feed in the study area nearly every day. Gulls were seen picking up food items from the soil in the low parts of the marsh. These activities occurred throughout the day and did not seem to occur at peak activity times. The possibility that feeding in the marsh was correlated with the tides was investigated in the following manner. The number of gulls feeding during the 5-min half-hour samples was compared to tide time. Tide time is defined as the number of half-hour intervals since low tide. Thus, if low tide was at 0700 and data are collected at 0930, the tide time is 2.5. Gulls fed during 28% of the sample periods. The correlation between the percent of samples in which gulls fed and the tide time is significant ($r = -0.71$, df $= 11$, $P < 0.01$, Fig. 8A). Gulls fed primarily at low tides. Considering only those sample periods in which gulls fed, the number of gulls feeding was highest at low tide (Fig. 8B). Gulls fed in the marshes more often when the tide was rising than when it was falling ($t = 3.72$, df $= 24$,

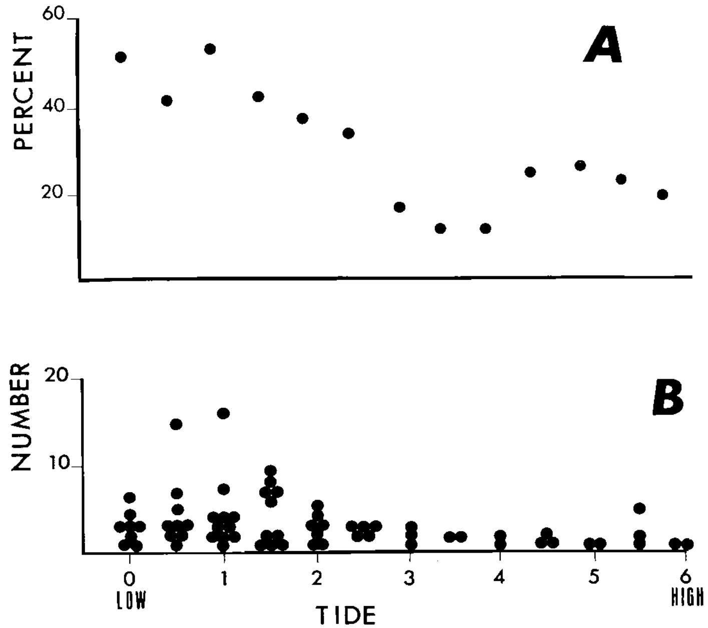

Fig. 8. Feeding activity as a function of tide time. A indicates the percentage of the samples at each tide time that contained some gulls feeding. B indicates the number of gulls that fed as a function of tide time for individual sample periods.

$P < 0.005$). Gulls fed in 45% of the sample periods during a rising tide, and during only 10% of the falling tide samples.

Post-egg

I marked 20 pairs of Laughing Gulls nesting in one area and studied their behavior in the 14-day period following egg-laying. The methods employed were the same as during the pre-egg period. In the half-hourly 5-min sample periods, I recorded the number of nests where both members of the pair were present. In Laughing Gulls the sexes share incubation and one member of the pair is always on the eggs. I also recorded the number of copulations, intruder displays, and trips for gathering nest material made each hour during the day.

Daily patterns.—At least one member of each pair was incubating at all times during the observation period. The mate is often present nearby or is away, presumably feeding. More pairs of birds were on their territories from 0600–0900 than from 1100–1400 ($t = 3.86$, df $= 51$, $P < 0.001$) and from 1600–1900 ($t = 4.1$, df $= 51$, $P < 0.01$). The number

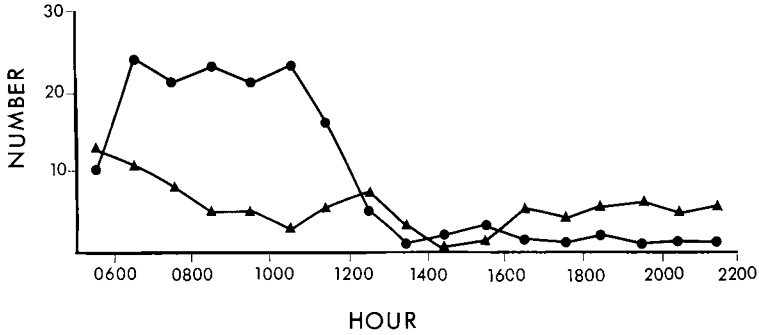

Fig. 9. Nest material trips (dot line) and intruder displays (triangle line) as a function of the hour of the day.

of pairs on territory from 1100–1400 is not significantly different from the number present at 1600–1900 ($t = -0.28$, df $= 51$).

Laughing Gulls add nest material continually during the incubation period. This is adaptive as many nests are periodically inundated by high tides. A substantial nest functions to keep eggs or young dry. Especially high tides result in increased nest building the following day. Most nest material trips occurred in the morning (Fig. 9). I expected this because the nonincubating bird brings back the nest material, and as I have shown above, the second member of the pair is more often present in the morning. A Student's t-test comparing the number of nest material trips from 0600–1300 with 1300–2000 showed them to be significantly different ($t = 2.79$, df $= 18$, $P < 0.001$).

At the initiation of egg-laying the frequency of copulations within pairs decreases, but the number of attempted rapes increases markedly. I define rape as when a nonmate mounts and tries to copulate with a female. All attempted rapes occurred while females sat on their eggs. Within the study area, only females were mounted and raped. As all birds in the study area were marked, the mounting by a nonmate was easily noted. The males who raped were often marked neighbors who had unsuccessfully courted their incubating mates, and then flown to a nearby nest to rape the incubating female. The number of rapes and copulations from 0600–1300 was not significantly different from the number at 1300–2000 ($t = 0.20$, df $= 16$). There was no daily peak in rapes and copulations during the incubating period.

When an intruder came within 3 m of the nest, the incubating gull usually gave an intruder display (Burger and Beer 1976). This display, which includes gakkering, usually repels the intruder. The number of intruder displays given did not vary markedly during the day (Fig. 9).

This is to be expected as well over 50% of the intruders are rapists and raping is evenly spaced throughout the day. As only 18% of the intruders are nest material stealers (Burger and Beer, 1976), the high level of nest material trips in the morning did not result in a significant increase in the intruder displays in the morning. The numbers of intruder displays given from 0600–1300 and 1300–2000 showed no significant differences ($t = 0.57$, df = 16).

Seasonal patterns.—Generally activity was low and decreased during the incubation period. The correlation between date and the total number of nest material trips per day was –0.73 (df = 10, $P < 0.01$). The correlation between date and the number of copulations and rapes per day was low (r = –0.58, df = 10, $P < 0.05$). The correlation between the number of intruder displays per day and date was –0.89 (df = 10, $P < 0.01$).

Discussion

The data presented can be organized to show patterns of variation in the activities of Laughing Gulls during the day and seasonally. Activities related to breeding (courting, copulating, fighting) increased during the 14-day period prior to egg-laying. Breeding activities such as copulation and rapes, nest material trips, and intruder displays decreased during the 14-day period following egg-laying. Maintenance activities (preening, swimming, bathing) remained constant during the period of study. A similar increase in courtship activities prior to egg-laying was noted for Franklin's Gull (*Larus pipixcan*) (Burger 1974). No other comparable studies on activity patterns in gulls have been published.

The high increase of rapes at the onset of incubation bears comment. I believe it may be a by-product of selection for a high rate of copulation just prior to egg-laying. Marked pairs were observed to copulate up to nine times per day just prior to egg-laying. In the week following the onset of incubation, males frequently returned to their nests, courted their mates unsuccessfully, and subsequently flew to a nearby nest and attempted to rape an incubating female. For the 20 pairs of gulls in my study tract, rapes never fertilized any eggs, as the females continued to incubate their already complete clutches. High tides wiped out clutches, but these birds continued to court one another, and the females copulated only with their mates. Selection for a high rate of copulation just prior to egg-laying may result in a high rate of "copulation drive" in males following egg-laying. As their females are unreceptive following egg-laying and are incubating, the males begin to rape other females.

The data also show a significant daily variation in the activities of breeding Laughing Gulls. Daily variations were found in the number of gulls on territory, courtship, copulation, and territorial defense. Activity peaks occurred from 0700–0800 and from 1800–1900, with a low at midday during the pre-egg period. These findings are what most experienced fieldworkers would expect. However, such patterns have rarely been documented quantitatively in field studies. Peaks in activities in the incubation period occurred only in the morning; no afternoon peak developed. The reasons for this change in activity are unknown.

At the start of this study I expected to find variations in the quantity of behavior, but not in the quality (i.e. duration of copulation) of that behavior. The lengths of copulations varied significantly during the day. Peak durations occurred at the same time as peak frequencies. Possible reasons for a variation in copulation durations may be (1) thermal stress in the middle of the day, (2) decreased social stimulation as a result of few copulating individuals, (3) fatigue or "drive" reduction, and (4) time-related variations in circulating hormonal levels. Thermal stress seems unlikely as an explanation as the copulation period extends from 9 May until 25 May when the marsh is still relatively cool and the birds do not exhibit any signs of thermal stress. Likewise, it is unlikely that the explanation lies in decreased social stimulation during midday because in the early part of the season when copulation frequency is low, the copulation durations during peak hours are as long as later in the season when many other gulls are also copulating.

Individual pairs exhibit the same activity pattern as the group. Individuals that first copulate during a peak period copulate for a long time, and those that first copulate during a low period usually copulate for a short time. Therefore, I feel it is unlikely that the activity pattern comes from a drive reduction. As males start copulating at different times of the day, they would also tire at different times of the day. Thus short copulations should occur at different times of the day. Such an asynchronous pattern would result in a constant mean duration of copulation at different times of the day. The data show a variable mean in copulation duration.

Possibly the copulation duration curve of the Laughing Gull may have a hormonal basis. The pattern exhibited may reflect a diurnal rhythm in female receptivity. Copulation in Laughing Gulls normally proceeds with the male mounted dorsally until the female begins to move slightly. In some cases the female walks out from under the male. I have seen males in this situation continue to wingflap and give the characteristic copulation call while on the ground.

Laboratory studies with Japanese Quail (Coturnix coturnix) indicate that receptivity in females depends upon circulating levels of estrogen and progesterone (Adkins and Adler 1972; Noble 1972, 1973). These investigators were interested in the effects of hormones on successive days and not on daily rhythms. Other studies have shown that there are daily rhythms in prolactin levels (Meier et al. 1969, Dusseau and Meier 1971, Meier and MacGregor 1972). A circadian sensitivity to prolactin levels has also been shown (Meier et al. 1971). Possibly the daily rhythm of copulation duration exhibited in Laughing Gulls in the field reflects a daily change in hormone levels. Such a conclusion must wait for experimental study in a laboratory where hormone levels can be determined.

My findings on the rhythm modulations of Laughing Gulls suggest that field biologists cannot collect data at one, a few, or haphazard times of the day and arrive at generalizations concerning the quantity or quality of that behavior without first examining how the behavior varies throughout the day. It is not sufficient to sample at only one time of day and infer behavior for the rest of the day. Similarly the existence of a daily variation in copulation duration brings into question studies in which a small sample size is used to determine the "mean" copulation duration.

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Summary

Adult Laughing Gulls were studied in the 14-day period prior to egg-laying and in the 14-day period after egg-laying to determine daily and seasonal rhythms of activity.

In the 14-day period prior to egg-laying, the number of birds present in the study area was significantly higher in the morning and late afternoon than it was at midday. Similarly, the percentage of birds engaged in courtship, copulation, and fighting was significantly higher in the morning and late afternoon than at midday. The duration of copulations also was significantly higher in the morning and late afternoon than at midday. This variation in the quality of behavior was unexpected.

In the 14-day period following egg-laying the pattern changed such that a peak in activity was noted in the morning but not at other times of the day.

Activities concerned with breeding (courting, copulating, fighting) in-

creased during the 14-day period prior to egg-laying. Breeding activities (copulations, rapes, nest material trips, and intruder displays) decreased during the 14-day period following egg-laying. Maintenance activities (preening, swimming, and bathing) remained constant during the period of study.

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