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TIME-PARTITIONING OF CLUTCH AND BROOD CARE ACTIVITIES IN HERRING GULLS: A MEASURE OF PARENTAL QUALITY?

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ABSTRACT.—Thirty-one Herring Gull (*Larus argentatus*) pairs were observed during incubation and brood care over three breeding seasons at a colony near Port Colborne, Ontario (42°53'N, 79°16'W). Parents that successfully raised two or more chicks (n = 17) were normally both present with the clutch during incubation. In most of these pairs, timing of incubation was partitioned such that each partner incubated most frequently at predictable times of the day. Similar attendance synchrony was recorded during the first 10 days of brood care. In other successful pairs, incubation and brood care were also partitioned equitably between partners. Conversely, in less successful pairs that raised at most one chick (n = 14), clutches and broods were frequently unattended by one or both parents. Synchronous or equitable partitioning of parental care activities were absent, with consequent egg and chick loss. Differential parental quality of pairs is inferred from these patterns.

Gull species (Laridae) are generally monogamous and both partners exhibit extensive parental care behavior during incubation and chick care periods. Among large-bodied *Larus* gulls, joint parental care is particularly important as egg and chick loss to conspecific neighbors can be substantial (Brown 1967, Parsons 1971). Thus, active participation by both parents may be necessary for chicks to be successfully raised.

Studies of several colonially nesting seabirds have revealed qualitative and quantitative sexual differences in parental activities during breeding (Burger 1981, Butler and Janes-Butler 1983). For example, Southern (1981) reported that male Ring-billed Gulls (*L. delawarensis*) were more agonistic toward intruders than females, an observation also noted for male Herring Gulls (*L. argentatus,* Morris and Bidochka 1982). Male Western Gulls (*L. occidentalis*) were more active in territorial defense (Hand 1986) and fed chicks more frequently than their female partners (Pierotti 1981). The approach used in all these studies was to pool data from all pairs to establish sexual differences during breeding.

My intention was to take an alternative approach. I observed the behavior of Herring Gull partners during incubation and brood care periods, and then examined parental contributions on a pair by pair basis. Specific objectives were (1) to record attendance patterns by partners during incubation and the first 10 days of chick age, and (2) to assess the relationship between patterns observed and the reproductive success of each pair.

METHODS

The Herring Gull colony was on an artificial breakwall 1 km off the north shore of Lake Erie near Port Colborne, Ontario (see Morris and Haymes 1977 for descriptive and photographic details). In each of 3 years, observations from an elevated blind, located on the periphery of the colony that numbered between 75–80 pairs, began in mid-April, prior to the initiation of the earliest clutch. The rock substrate is normally free of ice by early March, and although many pairs are present then, egg-laying by the earliest pairs began in mid-April in two of the three years (see Morris and Chardine 1985 for details of the exception).

I observed incubation and chick care attendance by partners of 8 pairs in 1979, 12 pairs in 1980 and 11 pairs in 1981. Study pairs were selected using the following criteria: (1) some identifying mark (aluminum ring, color band) on at least one member of each pair, (2) proximity to the observation blind (within a 15-m radius), (3) first eggs laid during a "peak" of egg laying at the colony, and (4) a completed clutch size of 3 eggs. Some individuals or pairs were observed in more than one year (see Results). Peak egg laying was arbitrarily defined as within ±1 SD of the mean date of first eggs laid by all pairs in the colony that year (cf. Morris and Chardine 1985). Clutches were inspected periodically during incubation and hatching by walking to all nests. A second observer was in the blind during such checks to note the behavior of adults during and following investigator activity in the colony. Chick survival in study broods was determined by observation from the blind.

Parental attendance data were taken almost daily each year during 3-h periods following sunrise or preceding sunset. These periods are known to be times of maximal activity by adult Herring Gulls at this location (Morris and Black 1980). For all single observation days, morning and evening observation periods were rotated such that the total numbers of hours in morning and evening time slots were approximately equal each year. At the beginning of most periods, two people entered the blind and one left immediately; behavior of the gulls was normal within 5 min of departure by the second person. Study pairs were scanned continuously through horizontal openings in the front and two sides of the blind taking care not to focus on any pair for more than a few seconds. Data on parental attendance were recorded directly onto a field sheet formatted to receive information for each pair. Records of attendance with their clutch or brood by members of each pair were recorded from laying of the first egg

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to the date when the youngest chick in the brood was 10 days old. During incubation, I recorded the sex of each incubating bird and the presence or absence of a standing mate. The sex of partners was based on courtship feeding and copulation activities observed early in each year. The presence or absence of the mate not incubating or attending chicks was determined with relative ease as off-duty birds normally occupied a characteristic location near the nest. The number of eggs hatching in each study clutch, and the number of chicks surviving to at least 20 days of age were determined each year.

RESULTS

Parental Reproductive Success

The 3-egg clutches of all study pairs were initiated between 28 April–14 May 1979, 20 April–2 May 1980, and 27 April–3 May 1981. In each year, these dates fell within 1 SD of the mean date of clutch initiation for all pairs in the colony. Based on reproductive performance, pairs were arbitrarily segregated each year into two relative categories of parental reproductive success (Table 1). "Successful" parents (n = 17) were taken as those that hatched 2–3 eggs, and had a minimum of 2 chicks survive to 20 days of age. Less successful parents (n = 14) were those that hatched 0–3 eggs, and had a maximum of 1 chick survive to 20 days of age. Successful and less successful pairs were distributed throughout the range of clutch initiation dates in each year. There was no tendency for either group of parents to initiate clutches before or after the mean date of egg laying (Mann Whitney U test, $n_1 = 14$, $n_2 = 17$, $U = 82$, $P > 0.1$).

Descriptive statistics (percentages, means ± 1 SD) for pairs in the successful and less successful parental groups were as follows. Forty-nine of 51 eggs (96%) hatched in clutches of successful parents, and 42 chicks (85%) survived to at least 20 days from these broods (2.47 ± 0.49 chicks per pair). None of these broods lost more than a single chick. Conversely, of 42 eggs laid by females of less successful pairs, 23 (54%) hatched, and single chicks survived to 20 days from only 8 broods (34%; 0.57 ± 0.48 chicks per pair). Three pairs abandoned their clutches about one week before eggs were due to hatch. Where known, the fates of eggs that did not hatch and the age of chicks that were lost are listed in Table 1.

Ten of the 23 pairs under observation in 1980 and 1981 were known to have changed ("change," 7 pairs) or retained ("same," 3 pairs) their mates from the previous breeding season. Previous-partner status of the other 13 pairs observed in 1980 and 1981, and of the 8 pairs observed in 1979, was unknown. Various combinations of successful and less successful status (as defined above) were achieved by "change" and "same" pairs in the second year. Of the 7 "change" pairs, 5 were successful in both years, 1 was less successful in both years, and 1 was less successful in the second year. Four birds known to have changed partners were male and 3 were female. Of the 3 "same" pairs, 1 was successful in both years, 1 was less successful in both years, and 1 achieved successful status in the second year. Thus, 6 of 7 "change" pairs achieved the same reproductive success status in the two years, while 2 of 3 "same" pairs did so. There was no difference in the distribution of pairs within these two categories of reproductive success (Fisher Exact Probability Test, $P = 0.94$).

TABLE 1
HERRING GULL PAIRS GROUPED ACCORDING TO HATCHING SUCCESS AND CHICK SURVIVAL TO 20 DAYS OF AGE[a]

	Parental pair category[b]		
	Successful	Less successful	
Year	(Hatched 2–3 eggs,[c] 2,3 chicks survived)	(Hatched 1–3 eggs, 1 chick survived)	(Hatched 0–2 eggs, no chicks survived)
1979	4	1	3[d,e]
1980	6	3	3[f]
1981	7	4	0

[a] 16 chicks lost between 1–10 days of age; 6 lost between 11–20 days.
[b] See text for average number of chicks fledged by pairs in each parental pair category.
[c] 15 of 17 pairs hatched all 3 eggs.
[d] All eggs in one clutch destroyed by male (Chardine and Morris 1983).
[e] Two clutches abandoned by parents late in incubation.
[f] One clutch abandoned by parents late in incubation.

Parental Incubation

Incubation time by each partner in each pair was determined as time spent incubating when the partner was gone, plus time spent incubating when both members of the pair were with the clutch (one incubating, one standing). The sum of these components during each hour of observation was used to determine the mean number of minutes per hour each partner spent incubating during morning and evening observation periods. During incubation, the mean observation time allocated to each of the 31 pairs was 48.9 ± 11.8 h.

Ten of the 17 pairs of successful parents exhibited an incubation pattern where one member incubated primarily in the morning while the partner incubated primarily in the evening (Fig. 1A). Incubation was either solitary with the mate gone, or more usually with the mate standing nearby. This "trade-off" pattern in the timing of incubation effort by mates was more strongly marked among some of the ten pairs, but was consistent among them all. There was no tendency for a particular sex to incubate in one time

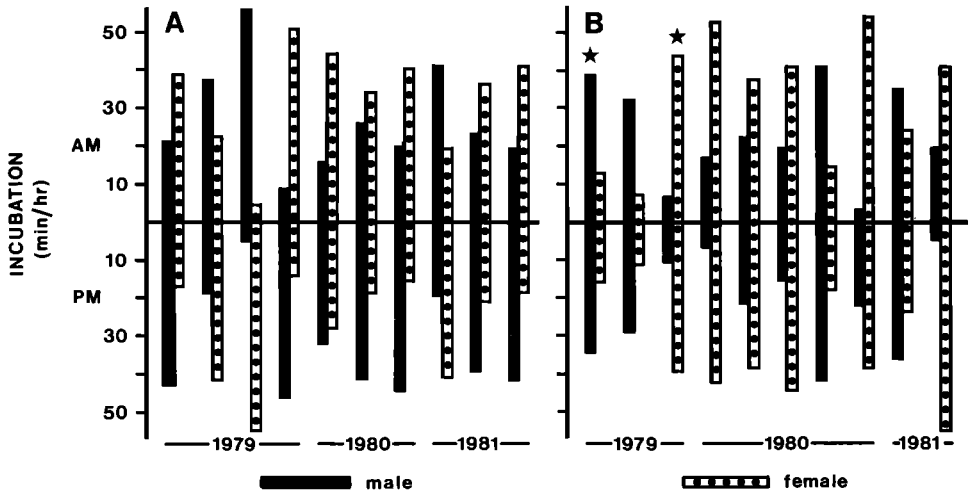

FIGURE 1. Time (mean minutes/hour) spent in incubation of 3-egg clutches by partners of Herring Gull pairs. A. Successful pairs, fledged 2–3 chicks. B. Less successful pairs, fledged 0–1 chick. (See text and Table 1 for further details.) The stars note pairs that abandoned their clutch late in incubation.

period or the other. In the other 7 successful pairs, one partner contributed more time to incubation than its mate in both morning and evening periods. In 4 pairs, the female contributed more to incubation duties, whereas in 3 pairs the male did so. However, the contribution to incubation by the partners was more equitable than disproportionate; the average incubation time each hour by the most committed member of the pair was only slightly more than 30 min (4 females, morning = 35.9 ± 4.1 min/h, evening = 36.9 ± 6.3 min/h; 3 males, morning = 34.2 ± 1.9 min/h, evening = 35.6 ± 1.3 min/h).

Contrary to the incubation behavior of successful parents, the timing of incubation by partners in 10 of the 14 less successful pairs revealed a quite different pattern (Fig. 1B). In each case, one parent incubated much more frequently than the other in both morning and evening periods, and there was no evidence of the incubation "trade-offs" observed between partners in many successful pairs. Of the remaining 4 pairs of less successful parents, data in 2 cases were too few (<10 hours each) to permit assessment; in the other 2 cases, partners did not follow any discernable pattern of incubation. Examples of the two principal types of incubation pattern used by successful (synchronous partitioning) and less successful (one partner heavily committed) pairs were observed in all three years (Fig. 1).

Finally, during our hours of observation, partners of 15 successful pairs were never simultaneously absent from their clutches. Partners from the other 2 pairs were both absent for less than 30 min in the over 40 h that each were observed. Conversely, mates of 6 less successful pairs were simultaneously absent for periods of time ranging from 2.8–10.2 h (an average of 19% of the total time each pair was observed during incubation). Three of these pairs abandoned their clutches about one week before eggs were due to hatch. In one case, the female contributed most extensively to incubation; in the two other cases, the males spent a disproportionate amount of time incubating in both morning and evening periods (see Fig. 1B for two cases).

Parental Attendance with Chicks

During the period of chick care, the mean time spent in observation of the 27 pairs that hatched at least one egg was 23.5 ± 4.1 h. In 10 pairs of successful parents, the partner that incubated primarily in the morning (or evening) was also primarily present with the chicks during the same time period. In each case, the partitioning of parental care activity observed during incubation was maintained during chick care. Mates in the 7 other successful pairs also continued to exhibit the time committment patterns of parental care during chick care that they earlier exhibited during incubation. An example of the pattern of attendance by mates of successful pairs is shown for male partners during morning (AM) observation periods (Fig. 2A). Similar positive correlations (Spearman Rank Correlation Tests) were found for three other comparisons of the timing of incubation and solitary attendance with chicks. These were (1) male incubation PM vs. male attendance with chicks PM ($r_s = +0.57$, $P < 0.05$), (2) female incubation AM vs. female attendance with chicks AM ($r_s = +0.74$, $P < 0.01$), and (3) female incubation PM vs. female atten-

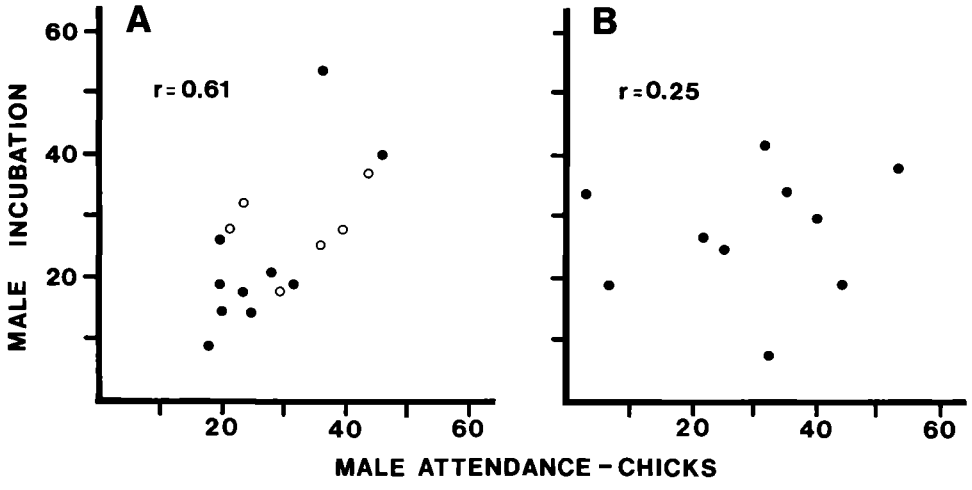

FIGURE 2. The relationship between time (mean minutes/hour) spent in incubation and time spent in solitary attendance with the chicks during the first 10 days of brood care. The example shown is for morning observation periods for male partners in Herring Gull pairs. A. Successful pairs (n = 16; incomplete incubation data available for one pair). B. Less successful pairs (n = 10; 4 pairs failed to hatch eggs). In A, closed circles are males of the pairs shown in Fig. 1; open circles are males from successful pairs where one partner exhibited somewhat more parental care activity than the other in both morning and evening time periods (see text for complete details).

dance with chicks PM ($r_s = +0.55$, $P < 0.05$). In each case, the correlations were based on 16 of the 17 pairs of successful parents; 1 pair had too few hours of observation during incubation for inclusion.

In contrast, these patterns were not observed among any of the less successful pairs for which data were available (n = 10). An example of the absence of correlation between incubation and attendance with chicks during morning observation periods is shown for males in less successful pairs (Fig. 2B). A similar lack of correlation was identified for two of the three further cases noted above (male-male PM, $r_s = +0.21$, $P > 0.05$; female-female AM $r_s = +0.22$, $P > 0.05$; female-female PM, $r_s = +0.57$, $P < 0.05$). In each case, correlations were based on the 10 pairs of less successful parents that hatched at least 1 egg.

DISCUSSION

The Herring Gull pairs observed in this study were segregated into two groups based on maximal differences in chick survival (see Burger 1986 for a similar procedure). Successful pairs realized a reproductive success rate (chicks fledged per pair) almost five times higher than that of less successful pairs. Less successful parents hatched fewer eggs, abandoned clutches, and lost chicks such that only 8 of 14 such pairs successfully raised a single chick. While these demographic measures of success were clearly different between the two groups, the pairs were similar in other respects. Females in all pairs laid 3-egg clutches during a colony-wide peak of egg laying early in the season each year. From other studies of larids, such individuals are known, on average, to represent an older, more experienced subset of birds in the colony (younger, less experienced larids produce smaller clutches later in the season). Some of the study animals were known to have bred in previous years; yet, despite other studies to the contrary (Coulson 1966, Mills 1973), there was no evidence among Herring Gulls at Port Colborne that "change" pairs were less successful than "same" pairs.

The patterns of parental attendance during incubation and chick care paralleled differences in the reproductive success of pairs in the two success categories. Successful partners were coordinated in their contributions to egg and chick care; less successful parents were not. Partners of 10 successful pairs were predictable in the time of day when care was given and were in synchrony with each other in the partitioning of time allotted to parental care activities. In the remaining 7 successful pairs, one mate spent somewhat more time incubating and attending chicks than the other. Rather than a "trade-off" pattern of parental care, partners exhibited general time equitability of care given to the clutch and brood. Equitability of time investment in incubation and chick care activities has elsewhere been suggested as characteristic of successful Herring Gull parents (Burger 1986). In either case, partners of

successful pairs in this study coordinated their parental care behavior such that joint absence was infrequent and contributions to egg and chick care were synchronized.

Conversely, in less successful pairs, one partner exhibited disproportionate contributions to incubation and chick care, and was the sole partner in attendance during much of the day. There was no evidence of synchrony or coordination in the timing of care given to eggs or to chicks, and in several cases, both partners were frequently absent simultaneously from the clutch or brood.

Sexual selection theory predicts that the greater investing sex (usually females) should be more discriminating in the choice of a partner than the less investing sex (usually males; Orians 1969, Trivers 1972). Burley (1977) extended sexual selection theory to predict within-sex variability with regard to selectivity toward mates. She showed that while female feral pigeons (*Columba livia*) were relatively more selective of mates than males, high quality males were selective as well. Among colonially nesting seabirds, total effort given to parental care activities by males appears to be equal (Pierotti 1981, Western Gulls; Butler and Janes-Butler 1983, Great Black-backed Gulls, *L. marinus*), or exceed (Montevecchi and Porter 1980, Northern Gannets, *Morus bassanus*; Burger 1981, Black Skimmers, *Rynchops niger*) that of females. While differing on "parental investment" and "mating effort" terminology, these studies agree that overall parental care contributions by male and female partners are similar. Both parents care for eggs and chicks and are important to the reproductive fitness of each other. Accordingly, high quality in a mate is in the best interest of both partners, and selection pressure for choice of a high quality mate likely acts on both sexes.

While monogamous partners both contribute to the care of offspring, sexual differences in investment often take different forms and occur at different times during breeding. Predictions about which sex might be more discriminating in choice of a mate are complicated by difficulties in defining the currency of investment allocated at different phases of breeding (Knapton 1984). Among seabirds, "typical" male and female roles are usually well defined, but principal contributions occur at different times or in different ways. For example, female Great Black-backed Gulls invested more time than males in territorial attendance and incubation whereas, males engaged more in agonistic behavior during the post-hatch period (Butler and Janes-Butler 1983). Similarly, while the agonistic behavior of female Western Gulls toward intruders was less extensive than that of males, the timing of such acts by females was considered to represent an important component of territorial defense investment by the pair (Hand 1986).

Among seabirds, then, when extensive parental contributions are given by both parents, males and females are both likely to assess the quality of prospective partners. Differences in within-sex parental quality have been inferred by investigators from various indicators including clutch size (Coulson and Porter 1985), differential adult mortality rates during the breeding season (Burley 1985), and differential courtship and chick feeding rates (Wiggins and Morris 1986). Cues reflecting quality are likely also available. For example, courtship feeding rates by males appear to provide females with cues to the quality of potential mates (Nisbet 1973, Niebuhr 1981, Wiggins and Morris 1986). Foraging for food likely entails greater energetic costs than remaining at the colony (cf. Pugesek 1981), yet courtship feeding is the most direct way a male can contribute to the quality of eggs produced by a female (Smith 1980). Accordingly, males should be selective as to which female they will offer food. Cues about female quality might also be available for use by males. For example, the number of aggressive acts by a female toward intruders, and her willingness to remain on the territory, may serve as indices by which a male can assess her quality as a reliable mate.

The results reported here indicate that differential mate quality appears to be expressed in attendance patterns of each partner during incubation and brooding. Previous work at the Port Colborne Herring Gull colony showed that joint absence or poor attendance by one partner resulted in increased loss of eggs and young chicks (Morris and Black 1980, Schoen and Morris 1983). In the present study, the timing of incubation by partners of successful pairs was a reliable predictor of the timing of solitary attendance with chicks. Synchrony in the timing of incubation attentiveness may, therefore, indicate to both partners the future willingness or ability of a mate to participate in brooding and protecting chicks. Ability to achieve synchrony in the timing of crucial parental care behavior suggests high quality in both partners. In colonial nesting Herring Gulls where cannibalistic neighbors are a persistent threat, some degree of parental cooperation is necessary for the survival of eggs and chicks. Failure by one partner to exhibit either synchronous or equitable incubation attentiveness, or to offer more than token attention to the clutch, probably indicates low parental quality of that individual. Early abandonment of the clutch by the most heavily investing partner may be a probable tactic in such cases, especially for young birds for which many

future breeding bouts are likely (see Pugesek 1981). It is noteworthy that clutch abandonment, by members of both sexes, was observed in three pairs about one week before eggs were due to hatch. In each case, one partner exhibited extensive periods of absenteeism during the 10–14 days after clutch completion while the "faithful" partner was incubating throughout much of the day (see Fig. 1B for 2 cases).

Coordinated parental care behavior, proposed here as characteristic of high quality parents, can be expressed in ways other than synchrony or equitability of time invested in clutch and brood care activities. Ability to achieve compatibility in foraging schedules (Niebuhr and MacFarland 1983), or in equitable resolution of conflicts over nest relief during incubation (Hand 1985), are also correlates that may be associated with high quality parents. However measured, the variability in parental quality identified among partners in my study was unlikely to be due solely to differences in age or in previous breeding experience. Indeed, study pairs were selected for similarity in clutch size and timing of clutch initiation in order to minimize these variables. In concert with studies to determine the overall role of the sexes in offspring care, detailed observations of particular pairs as reported here can provide insight into differential parental quality of the partners.

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