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Affiliation between the Sexes in Common Grackles

II: Spatial and Vocal Coordination

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With 13 figures

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Abstract

This study of the frequencies of activities performed by four breeding pairs of Common Grackles *Quiscalus quiscula* examined the behavioral regulation of partners' spatial association and vocal interactions and the possible effects of these interactions on the seasonal course and persistence of their affiliation. Spatial association of partners remained high until incubation began and then declined progressively. The ♀'s vocalizations when leaving the colony increased the chances that her mate would follow and thus promoted the pair's association. Song-answering, a form of antiphonal singing, was frequent only before the start of intensive nest-building and copulation. Measures of spatial association and frequencies of antiphonal singing were lower in pairs in which the ♀ chose her nest site early in the season, an indication that the behavior of younger and older pairs might differ. Differences in partners' interactions after choosing a nest site had no clear associations with differences in the seasonal development of their reproductive states or the persistence of their bond through incubation.

Introduction

Mated Common Grackles (*Quiscalus quiscula*, Icteridae) perform two characteristic responses to each other, following when the partner flies and answering the partner's vocalizations. This paper will consider the stimulus-response relationships that regulate these activities and the longer term consequences that these activities have for the partners' affiliation. A normative study can approach these questions by establishing the circumstances of partners' interactions and examining differences among pairs.

One consequence of heterosexual interaction is cumulative stimulation of the pair's reproductive development (ERICKSON and LEHRMAN 1964; LEHRMAN 1965; HINDE 1965; BROCKWAY 1969; NOTTEBOHM and NOTTEBOHM 1971; MARTINEZ-VARGAS and ERICKSON 1973; BARFIELD 1971; CHENG 1974), an effect that presumably occurs in many species with pair bonds (see BROWN 1967). These effects of heterosexual interactions on partners' endocrine states

depend strongly on the birds' previous breeding experience: more experienced individuals respond more rapidly to social stimulation (LEHRMAN 1962; LEHRMAN and WORTIS 1967). Partners' interactions might also affect the durability of their attachment to each other (see ERICKSON 1973).

Among pairs of Common Grackles, there is appreciable variation in the frequency of partners' interactions. The pairs also differ in the seasonal timing of their nesting and in the ♂'s fidelity to his mate through the incubation period (WILEY 1976). If the interactions of paired individuals directly affect the persistence of their affiliations or the seasonal development of their reproductive states, then, for birds with similar experience, the frequency of partners' interactions early in the season should correlate with the ♂'s fidelity to his mate or the seasonal timing of the pair's nesting behavior.

The results reported here suggest that differences in partners' interactions early in the season correlate with differences in the date of the ♀'s localization at a nest site. This finding is probably explained by differences in the birds' ages or previous experience, variables not assessed in this initial study. Differences in partners' interactions do not relate consistently to the ♂'s fidelity, although variation in the birds' ages might mask this effect. The results, in addition, elucidate the stimulus-response relationships that serve to regulate partners' activities.

Procedures

This field study focused on part of a large, well habituated colony in groves of pines on the grounds of the New York Zoological Society in Bronx Park, New York City (WILEY 1976). By standing quietly I could easily observe the birds from a distance of 5–10 m. Observations lasted from sunrise to about 10:00 on 41 mornings between 5 March and 26 May.

Beginning 31 March I recorded timed samples of the behavior of four identified pairs. I paid particular attention to vocalizations and to sequences of behavior as the pairs arrived and departed from the colony. Sampling periods, determined in advance, began and ended without reference to the birds' activities and usually lasted at least 30 min. This period ordinarily included several visits to the colony by the pair. The initial observation period each morning rotated among the pairs.

Behavioral events were recorded in their proper sequence in a short-hand notation. At irregular intervals, approximately every few minutes, the time was noted. With a little practice I could record, for one or two pairs at a time, the birds' locations and movements within the colony, their displays, and certain vocalizations.

In particular, I noted every song by each member of the pair, except during periods of intense activity, when I estimated the numbers of songs in each bout by using the following three categories: at least three, at least five, or at least ten. As these estimates were conservative, my figures for rates of singing are probably low on days when singing was frequent. This bias would tend to reduce any differences between birds or between stages in the nesting cycle.

Each time one or both of the birds arrived in or departed from the colony, I recorded the time and the sequence of events: which one flew first, whether the other followed, vocalizations before and after the first bird flew.

My samples thus allowed me to estimate the amount of time each bird spent in the colony, the frequencies of song and certain other displays, and the frequencies of various sequences of arrival and departure.

As described previously (WILEY 1976, in press), I could recognize individual ♂♂ and ♀♀ by their distinctive songs. After incubation began, a ♀ became much quieter, so that I usually had to identify an incubating ♀ by her association with a nest. As incubating ♀♀ normally went directly to their nests when returning to the colony, I rarely had difficulty following their behavior in the colony. While their mates incubated, ♂♂ also sang less frequently than earlier, and on rare occasions this resulted in my temporarily overlooking a ♂ present in the colony. Whenever I could follow ♂♂ continuously, social interactions with birds other than the mate always involved singing by the ♂. Normally the individualistic songs allowed quick recognition of any ♂ as soon as he arrived in the colony and often even before actual arrival.

Vocalizations and distinctive action patterns of this species are discussed elsewhere (FICKEN 1963; WILEY 1976, in press).

Stages of the Nesting Cycle

In analyzing the quantitative data on a pair's interaction, I have combined samples from a series of days in each of five characteristic stages of the nesting cycle. These five stages, described in more detail elsewhere (WILEY 1976), are separated by relatively clear changes in a pair's behavior. Stage I precedes the ♀'s localization at a nest site. Stage II continues until the ♀, within two or three days, constructs most of the nest cup. Stage III includes intensive nest-building (IIIa) and beginning a few days later copulation and egg-laying (IIIb). Stage IV begins with incubation and Stage V with the hatching of the young. ♀JJ laid her eggs too late for me to observe Stage V for this pair during my study. Pair D, whose nest was destroyed in a storm just after hatching, reverted to nest-building within a few days, in preparation for a second nesting attempt in the same nest. In the following account, Stage V for Pair D includes this period between the destruction of their first nest and the resumption of incubation for their second attempt. No samples were obtained for Pair B in Stage IIIb. Table 1 summarizes for each pair the numbers of samples from each nesting stage and the dates on which the pair was first and last observed in each stage.

Table 1: Numbers of timed samples of behavior and dates for each breeding stage for four pairs of grackles

	Stages of Breeding Cycle				
	I	II	III	IV	V
A. Principal Activity					
	Exploring	Localized at Nest - Site	Final Building and Copulation	Incubation	Feeding Nestlings
B. First and Last Dates Observed					
Pair G	Mar 31 - Apr 5	Apr 12 - Apr 23	Apr 26 - Apr 30	May 4 - May 14	May 17 - May 26
Pair D	Apr 2 - Apr 5	Apr 12 - Apr 16	Apr 19 - Apr 26	Apr 27 - May 10	May 17 - May 26 ^a
Pair JJ	Apr 12 - Apr 20	Apr 22 - Apr 30	May 4 - May 10	May 14 - May 26 (May 19) ^b	-
Pair B	-	Mar 31 - Apr 27	Apr 29 - Apr 30	May 5 - May 19 (May 10) ^b	May 21 - May 26
C. Number of Timed Samples					
Pair G	3	6	2,2 ^d	2,2 ^e	3 (1)
Pair D	2	4	2,3	3,3 (2) ^e	3 (1)
Pair JJ	1	4	2,2	1 (1), -	-
Pair B	-	9	2,0	1,3	1 (2)

^a Period following the destruction of Pair D's first nest by a storm. ^b Date ♂ last seen. ^c Parentheses enclose the number of additional samples excluded from most analyses because some departures or arrivals were overlooked. ^d Samples obtained during Stage IIIa (intensive nest-building) and during IIIb (copulation and egg-laying). ^e Samples obtained during the first and second half of incubation, Stages IVa and IVb.

The Four Pairs

The four intensively studied pairs differed strikingly in two respects: the permanence of the partners' affiliation and the timing of their nesting cycle during the season. ♂♂ G and D remained with their mates throughout incubation, while ♂♂ B and JJ had deserted by the middle of incubation. Desertion by the ♂ occurred frequently in this colony; about half of the ♂♂ whose mates nested in the grove of pines that I had under observation eventually deserted their mates (WILEY 1976). Desertion involved complete termination

of the ♂'s association with his former mate. In no instance did a deserting ♂ return later to help feed the nestlings.

Pairs showed little evidence of synchrony in their nesting cycles. Localization at a nest site occurred between March 31 and May 4 in the four pairs that I studied intensively (Table 1). Other pairs chose nest sites earlier and later than these dates. Stage III began between April 19 and May 4, incubation between 27 April and 14 May. Pair D was the first to begin incubation, Pair JJ the last. Pairs still explored for nest sites in the pine groves on the last days of my study and some began incubation in the last week. Some of these instances, not involving my intensively studied pairs, probably were second nesting attempts. The duration of Stage III (intensive nest-building and copulation) exhibited less variation than the durations of preceding stages in the nesting cycle. For Pairs G, B, and D, the known duration of Stage III amounted to 6-8 days. Pairs entered Stage III in the order D, G, B, JJ, and incubation began in the same order.

Spatial Coordination of Paired Grackles

Data from the timed samples of behavior permit several approaches to understanding the spatial coordination of paired grackles. Observations of the total time that one or both partners spent in the colony allow estimates of the proportion of time that partners remained together. Observations of arrivals and departures from the colony allow estimates of the partners' tendencies to follow each other. Figs. 1-7 present information for each pair about their time in the colony and their arrivals and departures during each stage of the breeding cycle.

Time spent in the colony

The four intensively studied pairs of grackles differed considerably in the amount of time that the partners spent together in the colony during the early morning (Fig. 1). Each pair's time together in the colony varied during the nesting cycle but these changes were not consistent from pair to pair. During intensive nest-building (Stage III a), a pair's visits to the colony were more often brief (< 4 min) than during other stages (X^2 values with $p < .05$ for Pairs G, D, and JJ). Because a pair made more frequent trips to the colony during this stage, the total time a pair spent in the colony decreased only slightly from Stage II.

A measure of a pair's tendency to stay together is the ratio of the time that the pair spent together in the colony to the total time that either one or both members were present. This ratio, presented in Fig. 2, provides an estimate for the probability that when one member of a pair was present in the colony both would be present.

Through Stage III all pairs except Pair B maintained high values, 79-98 %, for this measure of spatial association (Fig. 2). Although Pair JJ spent relatively little time near their nest during Stage III (see Fig. 1), their probability of being together remained high (Fig. 2). For Pair B, the proportion of time spent together increased substantially between Stages II and III, from about 50 % to about 80 %, an increase paralleled in other aspects of their behavior considered below.

Incubation placed constraints on the partners' tendencies to remain together. An incubating ♀ (Stage IV) averaged 70-85 % of her time on her nest during the first half of incubation and 85-95 % during the second half. Concomitantly, there was a substantial increase in the amount of time she spent alone (Fig. 3).

The rate of decrease in the ♂'s tendencies to stay with his mate during incubation determined whether or not his attachment failed completely be-

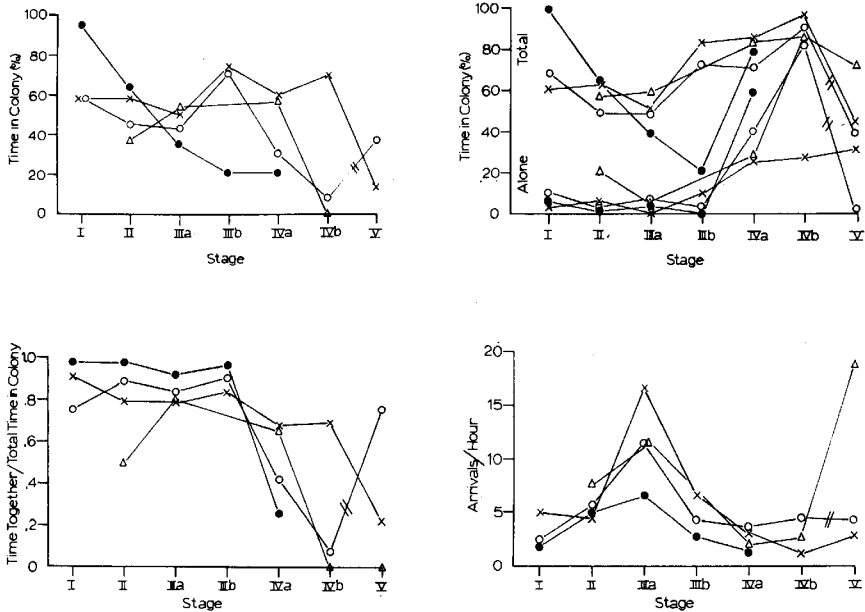


Fig. 1: Time that partners spent together in the colony as a percentage of the total time sampled between dawn and 10.00 h. Crosses, Pair G; open circles, Pair D; closed circles, Pair JJ; triangles, Pair B. Stages of the breeding cycle (I through IV) include the period of intensive nest-building (IIIa) and copulation (IIIb); for other details see text. Note that Stage V for Pair D corresponds to the period following the destruction of their first nest (see text)

Fig. 2: Probability that partners were together; the ratio of the time that both partners spent together in the colony to the total time that either one or both partners were present. For explanation of symbols, see Fig. 1

Fig. 3: Time spent in the colony by ♀♀ of four pairs. Upper four lines ("Total"), ♀'s total time in the colony as a percentage of time sampled; lower four lines ("Alone"), ♀'s time in the colony in the absence of her mate as a percentage of time sampled. For explanation of symbols, see Fig. 1

Fig. 4: Rate of the ♀'s arrivals in the colony for four pairs. For explanation of the symbols, see Fig. 1

fore incubation had ended. ♂♂ B and JJ, whose time in the colony decreased rapidly after the start of incubation, had deserted their mates by the middle of incubation. Although ♂ D remained faithful through incubation, he spent little time with his mate in the last half of incubation. Pair G's probability of being together, however, remained much higher through incubation than that of any other pair (Fig. 2). This pair spent more time together in the colony during incubation than they had during the stages preceding copulation (Fig. 1). Consequently, during incubation ♀ G spent only 25-30 % of her time alone in the colony (Fig. 3). ♂ G often perched quietly for long periods several meters from his mate's nest, while she incubated.

Once the eggs hatched, the coordination of Pair G dropped sharply, as the ♂ began to collect food for the nestlings. Pair D, whose nest was damaged soon after hatching, returned to behavior resembling that in Stage III a, during the initial period of intensive nest-building; the total time together in the colony (Fig. 1), the time spent alone by the ♀ (Fig. 3), and the proportion of time spent together (Fig. 2) all returned to levels close to those in Stage III a.

Arrivals in the colony

♀ usually visited the colony, with or without their mates, between 1 and 5 times per hour throughout most of the nesting cycle (Fig. 4). During Stage III a, during intensive nest-building, the ♀'s visits increased to 6-17 per hour. ♀ B, after her eggs had hatched, averaged over 18 visits per h as she collected food for her nestlings.

Another measure of a pair's tendency to stay together is the ratio of the number of instances that a pair arrived in the colony together to the total number of instances that either one or both arrived. This measure, presented in Fig. 5, provides an estimate for the probability that an arriving individual is accompanied by its mate.

The analysis of arrivals confirms the increased coordination of Pair B during Stage III as compared to earlier ($X^2 = 23.2$, corrected for continuity, $N = 113$; $p < .001$, one-tailed) and high coordination of Pair JJ through Stage III. Perhaps for Pairs G and D also, the tendency of partners to arrive together increased slightly from Stage II to Stage III a, although neither of these increases is statistically significant (Pair G: $X^2 = 1.163$, corrected for continuity, $N = 48$; $p = 0.1$, one-tailed).

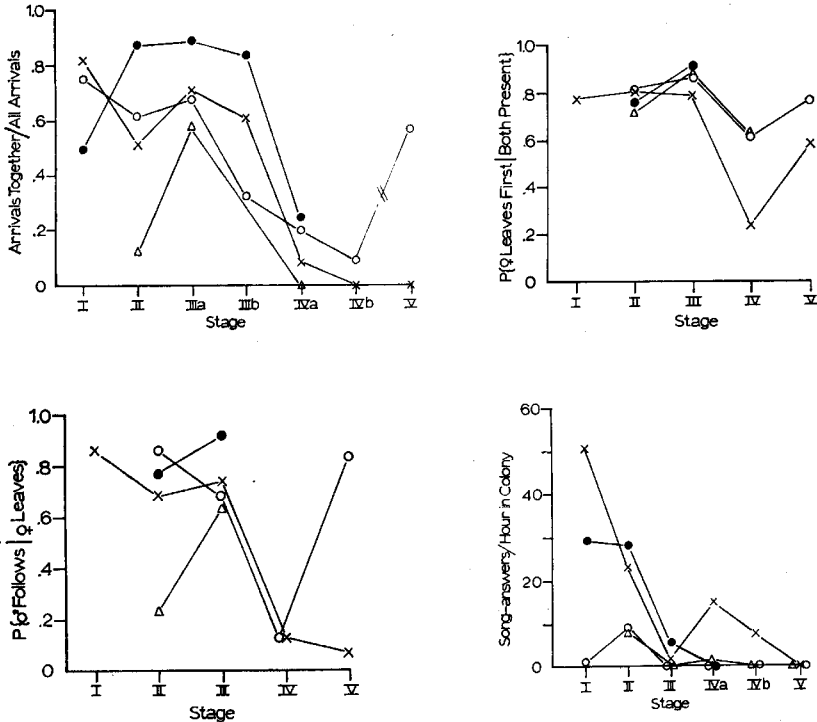


Fig. 5: Probability that partners arrived together: the ratio of partners' arrivals in the colony together to total arrivals either of one partner alone or both together. For explanation of symbols, see Fig. 1

Fig. 6: Probability that the ♂ followed when the ♀ left the colony in his presence. For explanation of symbols, see Fig. 1

Fig. 7: Probability that the ♀ left the colony first when both were present in the colony. For explanation of symbols, see Fig. 1

Fig. 8: Rate of vocal answering by four pairs. For explanation of symbols, see Fig. 1

It was my impression in the field that after a ♀ had chosen her nest site, the pair's interactions usually seemed less excited. This relaxation in the pair's behavior toward each other then changed to more intense interaction as nest-building and copulation increased. In accordance with this impression, the coordination of Pair G's arrivals in the colony decreased from Stage I to Stage II ($X^2 = 2.979$, corrected for continuity, $N = 44$; $p < .05$, one-tailed). The samples of arrivals for the other pairs during Stage I are too small for analysis.

The patterns of arrival in the colony confirm the decreased coordination of pairs during incubation. Although Pair G tended to stay together throughout incubation, as shown above, their arrivals in the colony after Stage III were rarely coordinated (Fig. 5). Pair D also dropped progressively in the coordination of their arrivals in the colony throughout incubation. After their nest was damaged, Pair D returned to a level of coordination comparable to that in Stage III a during their initial phase of nest-building.

Departures from the colony

When one member of a pair left the colony, the other often followed, another manifestation of the partners' attachment to each other. When the ♀ took flight in the ♂'s presence, during the stages preceding incubation, the ♂ normally followed her (Fig. 6). Pair JJ showed especially high coordination in this respect. ♂ B, on the other hand, followed his mate on fewer than 25 % of possible occasions during Stage II but greatly increased his following, to a level comparable to the other ♂♂, during Stage III ($X^2 = 6.26$, corrected for continuity, $N = 62$; $p < .01$, one-tailed). Similar trends, not statistically significant, appeared in the behavior of ♂♂ G and JJ but not ♂ D. There is an indication that ♂ G might have followed his mate less regularly during Stage II than during Stage I, a trend that parallels a decrease in this pair's tendency to arrive in the colony together.

During the incubation period, ♂♂ D and G followed their departing mates much less frequently than during earlier reproductive stages. Following the damage to their nest at the end of incubation, ♂ D returned to a high probability of following his mate.

The ♀ was less likely to follow the departing ♂ than vice versa. During Stage II the ♀ followed her mate on only 16 % of the instances that the ♂ took flight in her presence ($N = 30$). ♀ B showed even less coordination of this type than did the other three ♀♀.

Preceding incubation, the ♂ tended to wait for his mate before leaving the colony. Estimates of the probability that the ♀ would take flight first, when both members of the pair were present in the colony, remained high through Stage III (Fig. 7). From Stage II to Stage III this probability increased slightly ($X^2 = 3.81$, $N = 235$, $p < .05$, one-tailed), and Pairs B and JJ increased more than the other two pairs. As the ♀'s visits to the colony were not appreciably briefer than the ♂'s, this high probability of the ♀ leaving first when the pair was together in the colony reflects the ♂'s tendency to wait for his mate before leaving. Normally the ♂ then followed her. ♂ B during Stage II, however, usually remained behind, as indicated by the discrepancy between his low probability of following and the ♀'s high probability of leaving first.

During incubation the ♂ waited much less often for his mate before leaving. The relatively high probability that the ♀ would leave first when the pair was together during incubation resulted from her tendency to leave her

nest immediately after her mate landed nearby. In these instances the ♀ often responded to her mate's vocalizations (see below). During Stage IV ♀ G rarely left before her mate, because the ♂ now spent briefer periods in the colony than did his incubating mate. Following the hatching of their eggs, the probability that the ♀ would leave before her mate, when both were present in the colony, approached 50 %, as the two fed the young independently.

Spatial coordination: summary

These various measures of spatial coordination between the members of a pair largely agree in their representation of the pairs' interactions during the reproductive cycle. As expected, a pair's spatial coordination fell markedly during incubation. This drop was progressive, so that partners associated more during the first than during the second half of incubation. In addition, there are some indications that spatial coordination might have changed in minor ways during the stages preceding incubation, particularly a slight decrease in spatial coordination between Stages I and II, after localization at a nest site; and a slight increase from Stage II to Stage III, the period of intense nest-building and copulation.

A clear result from the observations of Pair D is the prompt rise in every measure of their coordination following the destruction of their nest just after the end of incubation. As they prepared for a second nesting attempt, these measures of their interaction returned to levels comparable to those in Stage III, their initial period of nest-building and copulation. This prompt change suggests that the decline in their coordination during incubation depended primarily on the external constraints on the ♀'s behavior.

The four pairs showed some striking differences in their patterns of spatial coordination. The decline in the partners' association during incubation proceeded at different rates for the four pairs, so that the partners of Pair G, and to a lesser extent Pair D, remained relatively well coordinated at the end of incubation, while Pairs B and JJ had completely dissociated. Pair B also differed from the others in their weak coordination during Stage II and the pronounced increase in their spatial association during Stage III, a trend less apparent in the other pairs. Pair JJ ranked high in most measures of spatial coordination during Stages II and III.

The substantially greater tendency for the ♂ to follow his departing mate than for the ♀ to follow the ♂ implies that the ♂ played the primary role in maintaining the pair's spatial association. Yet the ♀ clearly did contribute by following her mate on some of the occasions when he left first. The weak coordination of Pair B during Stage II is reflected in a lower tendency for the ♀ to follow the ♂, in comparison with the other pairs, as well as in a lower tendency for the ♂ to follow. The ♀'s contributions to the bond appear more clearly in the partners' vocal behavior.

Vocal Coordination of Paired Grackles

Vocal behavior during departures from the colony

When a paired grackle flew from the colony, it usually vocalized. ♀♀ often used Chaas in this situation, but Chacks were also frequent and Songs occasional. ♂♂ used Chacks or Songs almost exclusively. When the mate was present, it often answered immediately and followed. When one bird flew and the other followed and one or both vocalized, the sequence of

events was sometimes too rapid to record with certainty. In cases that I clearly observed, usually the ♀ flew and immediately vocalized, then the ♂ quickly followed either before or after vocalizing in response. Often the two birds' vocalizations overlapped. Probably all possible sequences occurred at one time or another: sometimes the follower called before the leader; sometimes the follower took flight before the leader called. In addition, even when the ♂ stayed behind after his mate took flight, he sometimes vocalized in response to her flight.

Table 2: Probability that the ♀ vocalized after taking flight

	Stage of Breeding Cycle		
	II	III	IV
A. ♂ Present in Colony			
Pairs G, D, JJ	.80 (50)	.73 (78) ^a	.92 (26) ^a
Pair B	.56 (46) ^b	.88 (16) ^b	.67 (3)
B. ♂ Not Present in Colony			
	II and III		IV
Pairs G, D, JJ	.64 (11) ^c		.89 (19)
Pairs B	.73 (15) ^d		.82 (11)

^a $\chi^2 = 3.145$, corrected for continuity, $p < .05$ (one-tailed). ^b $\chi^2 = 3.715$, corrected for continuity, $p < .05$ (one-tailed). ^c Not significantly different from the combined probability for these pairs during Stages II and III with the ♂ present; $\chi^2 = 0.95$. ^d Ditto; $\chi^2 = 0.42$.

When a ♀ left the colony during Stages II and III, she vocalized on about 70 % of all occasions, regardless of whether or not her mate was present in the colony (Table 2). When he was present at the time his mate took flight, he followed her more often when she vocalized in flight, with the exception of Pair B (Table 3). Although it was sometimes difficult to determine whether the ♂ flew before or after the ♀ vocalized, in clearly observed cases, as noted above, the ♀ usually vocalized before the ♂ took flight behind her. The restricted influence of the ♂ on the ♀ in these circumstances seems clear from the fact that ♀♀ vocalized about as frequently when leaving the colony in the absence of their mates as in their presence. The ♀'s calls evidently stimulated the ♂'s following.

Pair B interacted less in this manner than did other pairs. First, ♀ B vocalized less frequently when leaving the colony (65 % of instances instead of 75 % for other ♀♀). In addition, when she vocalized her mate was no more likely to follow than when she did not (Table 3).

The ♀♀ other than B vocalized slightly less frequently when leaving the colony during Stage III than during Stage II. Then during Stage IV, when the spatial coordination of pairs reached a minimum, ♀♀ vocalized on taking

Table 3: Probability that the ♂ followed according to whether the ♀ vocalized immediately after taking flight when the ♂ was present in the colony (Stages II and III)

	♀ Vocalized	No ♀ Vocalization
Pairs G, D, JJ	.91 (97) ^{a,c}	.35 (31) ^a
Pair B	.38 (40) ^{b,c}	.27 (22) ^b

^a $\chi^2 = 40.9$, $p < .01$. ^b $\chi^2 = 0.66$, $p > .25$. ^c $\chi^2 = 40.2$, corrected for continuity, $p < .01$.

flight more frequently than during any preceding Stage (Table 2). This high probability of calling when leaving her nest during incubation, readily apparent in the field, applied regardless of the ♂'s presence. After her eggs hatched, ♀ G's tendency to vocalize after taking flight decreased, particularly when her mate was absent. In contrast, ♀ D, after the damage to her nest at the end of incubation, continued her high rates of vocalization.

♀ B again differed from the others in the seasonal course of her behavior. During Stage II she called on only 59 % of her departures from the colony, but she increased to 77 % of instances during Stage III. Pair B's increased spatial association during Stage III thus coincided with the ♀'s increased probability of vocalization when leaving the colony.

Table 4: Probability that the ♂ vocalized after the ♀ took flight according to whether or not the ♀ vocalized and the ♂ followed (Stages II and III, four pairs combined)

	♂ Followed	♂ Did Not Follow	Combined
♀ Vocalized	.36 (103) ^a	.35 (34) ^b	.36 (137) ^c
No ♀ Vocalization	.12 (17) ^a	.22 (36) ^b	.19 (53) ^c

^a $\chi^2 = 2.86$, corrected for continuity, $p < .05$ (one-tailed). For Pair G alone, $\chi^2 = 5.32$, corrected for continuity, $p < .01$. For Pair B alone, $\chi^2 = 0.262$, corrected for continuity, $p > .50$. ^b $p > 0.1$. ^c $\chi^2 = 5.10$, $p < .01$.

A ♂ often vocalized after his mate took flight from the colony (Table 4). His probability of calling increased if he followed his mate and in addition if she also called. In clearly observed cases, the ♂ usually responded to the ♀'s calls rather than the reverse. In this behavior, ♂ B showed the same trends as the other ♂♂.

A ♂ also often vocalized immediately preceding his mate's departure. The promptness of the ♀'s response in these circumstances indicated that she had in fact reacted to her mate's vocalization. For pairs other than B, the ♂ vocalized immediately preceding nearly 25 % of his mate's departures during Stage II. This proportion fell to about 15 % during Stage III, while the ♀ engaged in frequent trips for nest material ($X^2 = 3.45$, $N = 128$, $p < .05$ one-tailed). ♀ B rarely took flight immediately after her mate's vocalization during any stage of the reproductive cycle. ♀ D reacted especially clearly to her mate's vocalizations during incubation. She regularly left her nest in response to her mate's song or call, particularly after he had just arrived in the colony. One half of her departures ($N = 16$) during incubation immediately followed her mate's vocalization. In these situations the ♀ clearly reacted to the ♂'s vocalizations.

Vocalizations thus helped partners to coordinate their movements. The ♀'s calls on taking flight from the colony apparently increased the chances that her mate would follow. Chaas or Chacks, broad-spectrum calls with sharp changes in amplitude, would provide excellent cues for locating the calling bird (KONISHI 1973; see WILEY in press). The effect of the ♀'s vocalizations on the ♂'s probability of following might depend entirely on their attracting his attention to his departing mate.

The ♀'s tendency to depart immediately after her mate's vocalization also seemed to increase the chances that he would follow her. Here the ♀'s reaction served to improve the pair's spatial association. By leaving immediately after her mate's vocalization, a ♀ might increase the likelihood that her mate is nearby and ready to follow.

In a noisy colony the efficacy of a vocalization in coordinating a pair would substantially improve if the vocalization were individually recognizable. The individual's songs clearly did include stable individual differences. Chaa and Chacks might also incorporate features diagnostic for individuals (WILEY in press).

Vocal answering

The most striking vocal coordination between paired grackles was Song-answering, a form of antiphonal singing. During these performances, each bird used its normal, individually distinctive song without modification. The interval between the start of one bird's song and the mate's answer lasted 0.25-2.5 sec (median, 1.52 sec; Q_1 , 0.56; Q_3 , 2.10; N , 13), and each bout included three to ten songs by each partner. Although the elapsed time between the two mates' vocalizations lacked the extraordinary precision found in the antiphonal singing of other species, these performances were nevertheless striking to hear. Early in the season, male Common Grackles normally accompanied their songs with Song-spread display, but later they employed less intense forms of this display or none at all during antiphonal singing with their mates (see WILEY, in press).

Song-answering occurred in bouts at irregular intervals while the pair visited the colony. After a pair landed in the colony, they sometimes engaged in Song-answering. It also occurred regularly after agonistic interactions with other grackles. Yet pairs also sang antiphonally without associations with other activities, as when both simply rested in the pines near their nest site. Both members of a pair also sang alone, and on occasion the two would both sing without apparent reference to the other's songs. Although pairs engaged in Song-answering normally perched 0.5-2 m apart, on occasion antiphonal singing between pairs occurred at much greater distances. Pair B once sang antiphonally while about 20 m apart. The only bird that sang antiphonally with an individual other than its mate was ♂ B, who eventually deserted his mate during incubation. On 26 March he briefly engaged in Song-answering with another ♀ in the absence of his mate.

Table 5: Rates of antiphonal singing by four pairs of grackles (Stage II)

	Mean Song-answers / Hour		Mean Songs / Hour Excluding Answers to Mate's Songs (And Proportion Answered by Mate)	
	Initiated by ♂	Initiated by ♀	♂	♀
Pair G	13.2	9.8 (43 %)	73.7 (18 %)	39.5 (25 %)
Pair D	2.0	6.8 (77 %)	51.2 (4 %) ^a	9.2 (74 %)
Pair B	6.4	1.9 (23 %)	80.7 (8 %)	4.2 (45 %)
Pair JJ	18.9	9.2 (33 %)	92.6 (20 %)	13.9 (66 %)

^a Includes abbreviated songs.

Either member of the pair could lead during Song-answering, although often one bird would lead repeatedly during any one bout. The ♀ answered a larger number of her mate's songs than he answered of hers (Table 5). Yet, in all pairs, the ♂ answered a far greater proportion of his mate's songs. The ♀♀, which sang much less frequently overall than their mates, actually did a large proportion of their singing during bouts of Song-answering. Most of the songs of ♀♀ B and JJ were answers to their mate's songs. ♀ G sang alone more than the other ♀♀, but still a large fraction of her songs was

in response to her mate's. ♀ D sang infrequently, either alone or in answer to her mate's songs. These data show that most of a ♀'s songs were responses to her mate and that her mate answered most of the rest of her songs. Consequently, the ♀'s tendency to sing had a major effect on the pair's frequency of Song-answering.

The incidence of vocal answering dropped strikingly from Stage II to Stage III, as intensive nest-building began (Figs. 8, 9, 10). Although the rates of Song-answering per hour during a pair's visits to the colony varied considerably on different days through Stages I and II, all pairs virtually ceased this behavior during Stage III.

On days with high rates of Song-answering during Stages I and II, Pair G tended also to have high measures of spatial association (Fig. 11). This concordance of spatial coordination and antiphonal singing, however, did not persist beyond Stage II.

Pairs B and D engaged in antiphonal singing much less frequently than the other two intensively studied pairs. Pair B's weak spatial coordination during Stage II accorded with their low levels of Song-answering. The infrequency with which Pair D sang antiphonally might relate to ♀ D's unusually infrequent singing in general.

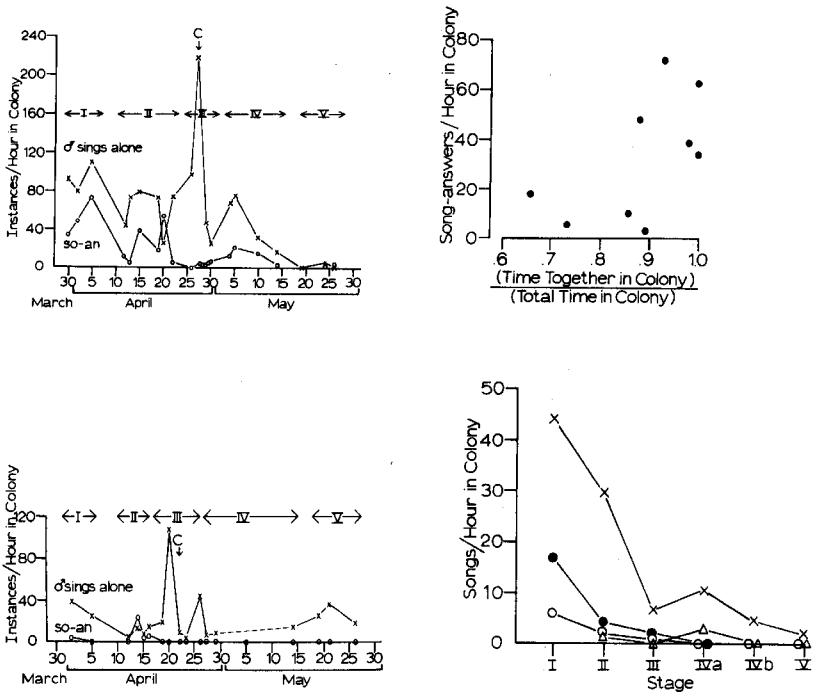


Fig. 9: Rate of singing alone by ♂ G (crosses) and rate of vocal answering (circles) by Pair G during the breeding season. Stages of the breeding cycle are indicated by arrows and numerals (I through V) at the top. C, date copulation first observed

Fig. 10: Rate of singing alone by ♂ D (crosses) and rate of vocal answering (circles) of Pair D during the breeding season. For further explanation, see Fig. 9

Fig. 11: Association of spatial coordination and vocal coordination by Pair G during Stage II. Ordinate, rate of vocal answering; abscissa, ratio of time together in the colony and total time that either partner was present

Fig. 12: Rate of singing alone by ♀ grackles in four pairs. For explanation of symbols, see Fig. 1

The slight resurgence of Song-answering by Pair G during incubation (Fig. 8) resulted from the ♀'s tendency to sing while on the nest. She often answered her mate's songs after he had remained silent for a while or when he returned to the colony after an absence. Their Song-answers during this period were led more often than previously by the ♂ (71 % during Stage IV, N = 42, 57 % during Stage II, N = 56). The ♂ answered a smaller proportion of the remainder of her songs (24 % in Stage IV, N = 49; 40 % in Stage II, N = 106). This evidence suggests that the persistence of antiphonal singing by Pair G during incubation depended primarily on the ♀'s tendencies to sing and to answer her mate's songs.

The seasonal pattern of the ♀'s singing, in contexts other than Song-answering (Fig. 12), closely paralleled the pattern for Song-answering. The frequency of song dropped markedly in Stage III, during intensive nest-building and copulation. Particularly for ♀ G the incidence of singing rose appreciably during incubation. The parallels between the frequency of Song-answering and the frequency of ♀ song in other contexts supports the notion that Song-answering depended strongly on the ♀'s tendency to sing. The low frequency with which ♀ JJ sang on her own, in contrast to the pair's high rate of Song-answering, reflected ♂ JJ's strong tendency to answer his mate's songs. Otherwise, when a ♀ sang infrequently alone, the pair engaged in little Song-answering.

The ♂ ♂'s rates of singing (Fig. 13), in direct contrast to the rates of antiphonal singing, increased sharply between Stage II and Stage III. This rise, for ♂ ♂ G, D, and JJ, resulted in a pronounced peak in their singing rates around the date of the pair's first copulation (Figs. 9 and 10), when Head-down display with song became frequent. As Song-answering dropped to trivial frequencies, the ♂ ♂'s singing rose to its highest levels.

Male singing decreased steadily throughout incubation. ♂ G maintained the highest rates of singing during this period, but after the eggs hatched and he began to collect food for the young, he ceased singing altogether. ♂ D, far more often than the other ♂ ♂, used Abbreviated Songs, resembling the initial segment of his Full Song (WILEY in press), in addition to his Full Songs. Although during the period before incubation the frequencies with which he used these two song-types paralleled each other closely (Fig. 13), during incubation his use of Abbreviated Songs soared to frequencies far above the singing rates for any ♂ in any reproductive stage. Probably these Abbreviated Songs represented lower motivational states. Possibly they substituted for other vocalizations, perhaps Chack or Brrts, that the other ♂ ♂ used under these conditions. In the field, though, I noticed no increase in the other ♂ ♂'s calls during incubation, so the sudden rise in ♂ D's Abbreviated Songs at that time perhaps had no clear analogue in the behavior of the other ♂ ♂.

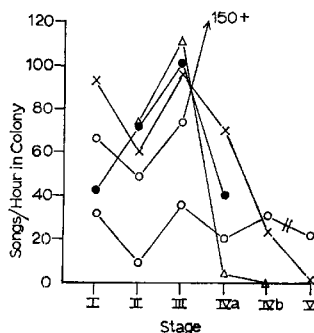


Fig. 13: Rate of singing alone by ♂ grackles in four pairs. For explanation of symbols, see Fig. 1. The upper line for ♂ D (circles) includes Abbreviated Songs, the lower line excludes them (see text)

Vocal coordination: summary

Seasonal changes in antiphonal singing showed some striking differences from other features of a pair's behavioral coordination. In particular, Song-answering dropped sharply at the start of Stage III, when spatial association between the pair reached a peak. Male song reached a peak around the time of the pair's first copulation, shortly after the sharp reduction in Song-answering. Thus antiphonal song played a major part in the pair's interactions only prior to the advent of intensive nest-building by the ♀.

Reciprocal Stimulation in the Regulation of Heterosexual Affiliations

In considering the dynamics of heterosexual affiliations, it is convenient to separate relatively short-term processes, primarily temporal and spatial coordinations in the pair's behavior, from longer processes, particularly the seasonal development of the pair's interactions. This arbitrary distinction separates interactions lasting seconds or minutes, which presumably depend on short-term stimulus-response relationships, from interactions over days or weeks, which can depend on cumulative effects of social interaction on the partners' endocrine states or on such durable external changes as the construction of a nest.

The regulation of partners' interactions, which produces coordinated behavior and an orderly progression of their affiliation, usually involves reciprocal reactions to each other, although coordinated behavior could also result from unilateral reactions by one individual to an indifferent partner or from reactions by both individuals to the same extrinsic cue. If the partners' interactions depended on a dual feed-back process, by which each would tend to optimize the behavior of the other by alterations in its own behavior, one or both comparators could require adjustment to insure stable interaction of these two feed-back systems (MACKAY 1969).

SCHNEIRLA and ROSENBLATT (1961) have stressed the importance of reciprocal stimulation in controlling the orderly progression of social interactions over periods of days or weeks, and theories of human social behavior have also emphasized "bicontingent" responses (PARSONS 1951). Reciprocal stimulation is an essential feature of TINBERGEN's early model for the short-term coordination of reproductive partners in fish with brief heterosexual affiliations. His model of reaction chains in stickleback courtship provided an hypothesis for the control of social dynamics solely through the immediate reactions of partners to each other (TINBERGEN 1951). A strict interpretation of this model does not accord with the stochastic nature of the individual's interactions (MORRIS 1958; NELSON 1964). However, MORRIS's (1958) diagrams suggest that even in the few minutes that ♂ and ♀ sticklebacks interact prior to spawning, the stochastics of their interactions probably change progressively, and such changes could depend on the cumulative effect of a reciprocal exchange of stimulation between partners.

The short-term social dynamics of paired Common Grackles, as measured during my hour-long observation periods, clearly involve partners' reciprocal reactions to each other. Vocal answering is performed reciprocally; each partner answers a proportion of the other's songs. Furthermore, the fact that Song-answering tends to occur in bouts suggests that the second partner's answer stimulates the first to sing again after a short pause. Spatial coordination also depends on reciprocal interactions. Although the ♂ usual-

ly takes the role of following, the ♀ will also follow her departing mate. In addition, the ♀ often departs from the colony in immediate response to her mate's vocalization.

Certain features of an individual's behavior, although evoking reactions from the partner, seem not to occur in response to the partner. In such situations the actions of one partner are independent of the other's. Thus when a ♀ vocalizes on taking flight from the colony, her mate, if present, is more likely to follow her. Yet the ♀ vocalizes no more or less often when her mate is present than when he is not. In this case, since the departing ♀ probably cannot determine with certainty the ♂'s presence or absence, probably her best strategy is to play it safe by vocalizing, regardless of the ♂'s behavior.

The reciprocal effects of the partners on each other during singing remain incompletely analyzed. The data in Table 5 suggest that the ♀'s frequency of singing first or alone correlates directly with the frequency with which her mate answers her: the more often the ♀ initiates song, the more often her mate answers. The causality here is probably complex; when the ♀ sings more often, the ♂ has more opportunities to answer and also is perhaps more stimulated to answer; conversely, the more often the ♂ answers, probably the more stimulated the ♀ is to sing. The data suggest that ♂♂ might reach a maximum rate of answering their mates' songs, at about 10 times per hour, even when the ♀♀ sing much more frequently. To compound the complexities, the ♀'s rate of answering her mate's songs shows no clear relation to the ♂'s rate of answering her songs or to her own rate of singing other than in answer to her mate. Experimental intervention will be necessary to unravel the reciprocal regulation of these coordinated vocalizations.

The Effects of Antiphonal Singing

THORPE (1972) has suggested that antiphonal singing might have any of four effects: (1) maintenance of contact between partners when out of sight; (2) mutual stimulation of partners' physiological state or maintenance of their affiliation; (3) territorial defense, in cases when neighboring individuals duet; and (4) mutual reassurance after a pair has engaged in a dispute with another pair. These four effects, which include both short-term and long-term processes, were proposed largely on the basis of the contexts in which antiphonal singing occurred, including the identity of the singers, their spatial relationships, and their immediately previous experience.

Common Grackles, like the shrikes described by THORPE and the HOOKERS (HOOKER and HOOKER 1969; THORPE 1972), often sing antiphonally after agonistic encounters with other pairs. On the other hand, they do not normally sing antiphonally when the partners are out of sight of each other or even very far apart, nor do they sing antiphonally with neighboring birds not their mates. I conclude that antiphonal singing of Common Grackles does not serve to maintain immediate contact between partners. The calls used when taking flight from the colony, on the other hand, certainly appear to have this effect.

The association of antiphonal singing with Stages I and II of the breeding cycle suggests instead that the cumulative effects of this vocal coordination might influence the seasonal development of the pair's internal states that lead to intensive nest-building, copulation and ovulation. Song-answer-

ing occurs primarily during the stages of the pair's affiliation prior to the onset of intensive nest-building and copulation. Once intensive nest-building begins, the progression of the pair's breeding behavior becomes much more predictable (WILEY 1976). At this point, although spatial coordination of the pair increases somewhat and the ♂'s singing rises sharply, antiphonal singing becomes a trivial component of their interactions.

Behavioral Interaction and the Date of Choosing a Nest Site

In a number of species, the retention of mates between successive nesting attempts and the seasonal timing of nesting vary with the partners' ages and previous experience breeding together (COULSON and WHITE 1958; COULSON 1966; DELIUS 1965; LERESCHE and SLADEN 1970; MILLS 1973). In this study, the ages and previous experience of my subjects were not known. It seems likely, however, from observations on other passerines (PERRINS 1970; SNOW 1958), that variation in the seasonal timing of nesting correlates with the age of one or both partners.

The ♂'s fidelity through incubation might also relate to the ages or previous experience of the partners. Circumstantial evidence against this possibility in Common Grackles comes from the fact that the ♂'s fidelity seemed to have no clear association with the seasonal timing of the pair's nesting. Pairs B and JJ, the two with deserting ♂♂, entered Stage II first and last among the four intensively studied pairs. These two pairs were the last two to enter Stage III among these four pairs, but other pairs with ♂♂ that deserted began Stage III earlier than Pair G. In the Common Grackles that I studied, the bond dissolved before the end of a complete nesting cycle, whereas the correlation of mate retention with age in other species has applied to breaks in the pairs' affiliations between complete nesting cycles.

The seasonal timing of the pairs' breeding, particularly the last date on which the ♀ engaged in exploring behavior in the pines, correlated with a number of measures of the partners' interactions. Vocal coordination paralleled spatial coordination in its association with these differences in the date of choosing a nest site. The pairs' rankings both for their frequency of antiphonal singing during Stage II (Fig. 8) and for the proportion of time spent together (Fig. 2) match their rankings for the date on which the ♀ last showed exploring behavior (for each pair of variables $r_s = 1.0$, $p = .05$, one-tailed). Thus pairs in which the ♀ chose her nest site earlier in the season showed less intense vocal and spatial coordination in these two measures during Stage II. Possibly these ♀♀ were older and knew their mates from previous years.

Differences in the birds' previous experience might mask an effect of partners' interactions on their reproductive development during Stage II. The relationship expected as a result of this effect does obtain among the three presumably older pairs, B, G, and D, although three pairs are not sufficient for a reliable conclusion. These three pairs stand apart from Pair JJ in the early date of the ♀'s localization at a nest site (Table 1; WILEY 1976). For them, the probability of arriving in the colony together and the proportion of time spent together in Stage II varies inversely with the first date of intensive nest-building. The frequency of Song-answering, on the other hand, is not related to the first date of intensive building.

The coordination of partners showed some indications of decreases between Stage I and Stage II, as they acquired a nest site. Pair G, the most adequately studied pair during Stage I, decreased their frequency of antiphonal singing, their arrivals together as a proportion of all arrivals, and the probability that the ♂ followed his mate when she left the colony in his presence. Less adequate data from Pairs JJ and D support these trends in some measures but not others. In gulls also, partners' interactions wane in intensity after the initial stages of pair formation (TINBERGEN 1953; BROWN 1967). Once a pair had localized their activities in the colony around a presumptive nest site, they could probably maintain the continuity of their affiliation with less persistent spatial association. Two factors thus could somewhat reduce the need for coordinated behavior between partners as the season progressed: the pair's improved adjustment to each other; and the establishment of a definite spatial focus for their activities.

Behavioral Interaction and Persistence of the Affiliation

The two pairs with deserting ♂♂ exhibited opposite tendencies in many of the partners' early interactions. Pair B ranked lowest of the four pairs and Pair JJ ranked highest in several measures of spatial and vocal behavior during Stage II: frequency of Song-answering; arrivals together as a proportion of all arrivals; probability of being together; and total time together in the colony. Pair B ranked lowest of the four pairs in two other measures of interactions: the ♀'s frequency of singing, and the probability that the ♂ followed when the ♀ left the colony in his presence. In most of these measures, Pair B dramatically increased their coordination during Stage III, so that their behavior during this stage much more closely resembled that of the other pairs.

Pair B and Pair JJ resembled each other during Stage II in the ♂♂'s high rates of singing, the low proportion of Song-answering initiated by the ♀, and a slightly lower probability of the ♀ leaving first when the pair was together in the colony. ♀♀B and JJ sang in answer to their mates more often than they sang first or alone (Table 5), in contrast to the other two ♀♀. The low proportion of Song-answers initiated by the ♀♀ in these pairs evidently resulted from this tendency to do most of their singing in answer to their mates.

The low coordination of Pair B during Stage II accords well with the ♂'s prompt desertion of his mate during incubation. This pair had well developed spatial and vocal coordination only for the relatively brief period of intensive nest-building (Stage III a). Although my observations did not include samples from their period of copulation (Stage III b), immediately preceding incubation, their close coordination presumably continued through this stage. Their lower coordination during Stage II resulted from reduced responsiveness of both partners to each other.

The differences between Pairs B and JJ might relate to the extreme differences in the seasonal timing of their nesting. ♀ B localized her activities at her future nest site late in March, one of the first ♀♀ in the colony to choose a site. ♀ JJ, in contrast, vacillated until the third week of April, after most ♀♀ in the colony had started their nests. This extreme difference in the ♀♀'s readiness to settle at a nest site might reflect a difference in their ages or previous breeding experience. Possibly the intense interaction of Pair JJ also reflected the first affiliation of a young ♀.

There are only a few indications that ♂ JJ, like ♂ B, responded less intensively or consistently to his mate than did the other two ♂♂ to their mates. During Stage II, Pair JJ ranked third and Pair B fourth in the probability that the ♀ left the colony first when the two were together. In other words, the ♂ often left before his mate. These differences among the pairs, however, were small. ♂♂ B and JJ, alone among the four intensively studied pairs, directed Head-down displays to ♀♀ other than their mates (WILEY 1976).

Pair G, the one that remained most closely associated through incubation, exhibited persistently high coordination through the early stages of their association. A characteristic of this pair was the ♀'s frequent singing, both in answer to her mate and either first or alone.

The other pair with a faithful ♂, Pair D, closely paralleled Pair G in measures of their spatial association. On the other hand, they resembled Pair B in the infrequency of their antiphonal singing. In addition, their Song-answers were overwhelmingly initiated by the ♀, which reflected a strikingly low tendency for the ♀ to respond to her mate's songs.

Two problems might have masked an association between the early interactions of a pair of Common Grackles and the subsequent faithfulness of the ♂. First, this initial study could not establish the ages and previous experience of the subjects. A long-term study might reveal consistent predictors of ♂ faithfulness among pairs with comparable previous experience. In addition, although most of my measures of behavioral coordination among pairs depended on the behavioral tendencies of both partners, dissolution of the affiliation might in some cases depend only on the tendencies of one partner. As shown earlier, the spatial coordination and, even more clearly, the vocal coordination of paired Common Grackles depends on the tendencies of both partners. The intensity of Pair JJ's interactions thus might have depended more on the ♀'s enthusiasm than on the ♂'s. In such cases, only experimental intervention can isolate the behavioral tendencies of any one subject from those of its social partners.

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Summary

A quantitative field study of the behavior of four pairs of Common Grackles (*Quiscalus quiscula*, Icteridae) examined the spatial and vocal coordination of partners in relation to the persistence of their affiliation and the seasonal timing of their nesting. Changes in partners' spatial and vocal coordination were documented over a three-month period through all stages of the breeding cycle.

Spatial coordination, primarily a consequence of the ♂'s following the ♀ when she left the colony or returned, remained high through the period of copulation and egg-laying but declined steadily through incubation. One

pair (B), with a ♂ that deserted during incubation, showed poor spatial coordination earlier in the season but increased their coordination once the ♀ began intensive nest-building. A ♀ also tended to follow her mate when he left the colony ahead of her, so the partners' spatial association did not depend entirely on the ♂'s initiative.

When the ♀ vocalized on leaving the colony, her mate was more likely to follow her. Again Pair B showed less coordination prior to intensive nest-building than did the others: the ♀ vocalized less often when she flew from the colony; and the ♂ followed no more often when she vocalized than when she did not.

Song-answering, a form of antiphonal singing, the partners' most striking form of vocal coordination, was only frequent prior to intensive nest-building and copulation. Although the frequency of singing by the ♂ reached its peak during the stage of copulation, antiphonal singing dropped to insignificant frequencies at this time. Changes in the frequency of antiphonal singing during the breeding cycle correlated with changes in the ♀'s tendency to sing. Both members of the pair answered the other's songs, however, so the frequency of antiphonal singing depended on the tendencies of both partners. In both pairs (B and JJ) with ♂♂ that deserted during incubation, the ♂♂ answered their mates proportionately less frequently than in the other two pairs.

The date on which the ♀ localized her activities at a nest site accorded with measures of the pair's spatial coordination (proportion of time spent together) and vocal coordination (frequency of antiphonal singing) in the period between localization and intense nest-building. Pairs that chose nest sites later interacted more intensely in these regards than pairs that settled earlier. This association is perhaps explained by differences in the ages or previous experience of early and late settlers.

The two pairs with deserting ♂♂ differed diametrically in many measures of the partners' coordination. An association of the quality of the partners' interactions and the ♂'s fidelity is perhaps masked by differences among the pairs in age and previous breeding experience. In addition, both spatial and vocal coordination between partners depended on the tendencies of both partners, while the persistence of the bond through incubation might have depended primarily on the tendencies of the ♂ alone.

Zusammenfassung

Die vorliegende quantitative Feldstudie untersucht an Pärchen von *Quiscalus quiscula* (Icteridae) die Bedeutung der räumlichen und vokalen Koordinierung beider Partner für das Aufrechterhalten der Bindung und für die Regulierung des jahreszeitlichen Rhythmus ihres Nistens.

Die räumliche Koordinierung, in erster Linie dadurch hervorgerufen, daß das ♂ dem ♀ folgte, wenn dieses die Kolonie verließ oder dorthin zurückkehrte, war hoch während der Kopulations- und Legeperiode, nahm hingegen während des Brütens ab. Eines der Pärchen (B), von dem das ♂ das ♀ während des Brütens verließ, zeigte am Anfang des Zyklus schlechte räumliche Koordinierung, die sich jedoch verbesserte, als das ♀ mit intensivem Nestbau begann. Ein ♀ neigte dazu, dem ♂ zu folgen, wenn dieses die Kolonie verließ; die räumliche Koordinierung der beiden Partner hing also nicht nur von der Initiative des ♂ ab.

Wenn das ♀ beim Verlassen der Kolonie rief, war es wahrscheinlicher, daß das ♂ ihm folgte. Auch dabei zeigte Pärchen B vor der intensiven Nestbau-Periode geringere Koordinierung als die übrigen Paare: das ♀ rief seltener, wenn es von der Kolonie wegflog, und das ♂ folgte ihm auf Rufen nicht öfter, als wenn es nicht rief.

Der „Antwort-Gesang“, die auffallendste Art von vokaler Koordinierung der beiden Partner, war nur vor dem intensiven Nestbau und vor der Kopulation häufig, obwohl das ♂ während der Kopulationsperiode am häufigsten sang. Bei den beiden Pärchen (B, JJ), deren ♂♂ das ♀ während des Brütens verließen, antwortete das ♂ dem ♀ seltener als bei den anderen Pärchen. Der Zeitpunkt, zu dem das ♀ den Nistplatz wählte, hing mit der räumlichen (Anteil der miteinander verbrachten Zeit) und mit der vokalen (Häufigkeit des Antwort-Gesangs) Koordinierung des Pärchens in der Zeit zwischen Finden des Nistplatzes und intensivem Nestbau zusammen. Pärchen die ihren Nistplatz später wählten, zeigten diese Verhaltensformen intensiver als jene, die dies früher taten. Vielleicht ist das aus dem Altersunterschied und der verschiedenen vorherigen Erfahrung früher oder später sich niederlassender Pärchen zu erklären. Beides mag auch den Zusammenhang zwischen dem Ausmaß der Koordinierung der Partner und der Treue des ♂ in den beiden Fällen verdeckt haben, in denen die ♂♂ die ♀♀ verließen. Räumliche und vokale Koordinierung der Pärchen hängen von den Bereitschaften der beiden Partner ab, während das Bestehen der Paarbindung während der Brutperiode möglicherweise vornehmlich vom ♂ allein abhing.

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