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Affiliation between the Sexes in Common Grackles

I: Specificity and Seasonal Progression

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With one figure

Received: 7. 1. 1975

Abstract

Heterosexual affiliation involves behavioral mechanisms that limit bond membership and regulate partners' interactions. Among Common Grackles, *Quiscalus quiscula*, two characteristic activities of partners, following and vocal answering, develop during group activities and promote the individual specificity of pair bonds. Pairs differ substantially in the durations and seasonal timing of the early stages of nesting activities and in the ♂'s fidelity to his mate through incubation. After the relatively abrupt start of intensive nest-building, the seasonal course of a pair's behavior becomes more regular, an indication that this transition in the ♀'s state is critical in pacing the pair's breeding activities. Aggression serves primarily to adjust the spatial relationships of individuals, both between partners and between unpaired birds. ♂♂ that deserted their mates during incubation had earlier performed precopulatory displays to other ♀♀.

Introduction

Heterosexual affiliation is the principal feature of social structure among breeding Common Grackles (*Quiscalus quiscula*, Icteridae). Pairs nest in diffuse colonies, often in groves of conifers near water, and show little indication of territoriality. Pair formation occurs in flocks that gather near colonies early in the season. Partners perform displays reciprocally, often termed mutual display, and follow each other in their trips to and from the colony (PETERSEN and YOUNG 1950, FICKEN 1963, WIENS 1965, SNELLING 1968, MAXWELL 1970).

The present paper analyzes the pair bonds of Common Grackles in relation to two topics in studies of the behavioral basis for social affiliations: the limitation of bond membership and the regulation of the partners' interaction.

Limitation of bond membership

In forming heterosexual affiliations, the partners' reactions are normally restricted to the appropriate species and sex and to particular individuals. These limitations on bond membership result from stimulus-specific responses that restrict an animal's interactions.

Previous attempts to compare pair formation in different species have concentrated on differences in species-specific and sex-specific responses (for example, LORENZ 1935). TINBERGEN (1939) emphasized the importance of sex-specific morphology that allows initial recognition of sex and species by interacting individuals. Especially in monomorphic species, recognition of sex in initial encounters depends strongly on sex-limited behavior. Often in such species a ♂ attacks or threatens any approaching conspecific, but only an unmated ♀ responds with appeasement behavior. The ♂'s "second reaction" then depends on the other individual's sex. Many fish and birds exemplify this kind of pair formation (NICE 1943, BAERENDS and BAERENDS-VAN ROON 1950, TINBERGEN 1959, NELSON 1965, DELIUS 1965, McMILLAN and SMITH 1974). In some monomorphic species, pair formation can involve a prolonged period of similar responses by the partner (TINBERGEN 1939), yet some initial sex-limited behavior or morphology must insure that the bond is normally heterosexual. The general condition for a heterosexual limitation on pair bonds then is a combination of some sex-limited features either of behavior or morphology and specific reactions to these features by at least one sex.

Because the initial interactions of partners often include aggression or threat, LORENZ (1935) proposed that in some species a dominance relationship established in these early stages produces the sexual differences in the partners' behavior. LORENZ noted that in captivity dominant ♂♂ of certain species treat subordinate ♂♂ in much the same way that they treat ♀♀, and subordinate ♂♂ often employ appeasement behavior similar to that of ♀♀. Later studies have confirmed that agonistic behavior is normal during pair formation in many species, although the relative roles of the ♂ and ♀ sometimes change during the season (HINDE 1954, 1955—56). However, it is not clear whether a dominance relationship within pair affiliations results from, or causes, sexual differences in behavior.

In addition to the heterosexual and conspecific restrictions on reproductive bonds, there are individual constraints. The restriction of an affiliation to particular individuals requires behavior that results in continued interaction between partners and exclusion of other individuals from the affiliation. Continued interaction with a partner could be facilitated both by individual recognition of the partner's behavior or morphology and by association of the partner with particular external referents, such as a nest site or territory (TINBERGEN 1953, NELSON 1965, DELIUS 1965). Whenever individuals have widely overlapping ranges, the continued association of bonded partners might require individual recognition independent of location, a capability that has been demonstrated in many birds (BEER 1970, BERTRAM 1970, BUTTERFIELD 1970, MORRIS and ERICKSON 1971, STETTNER *et al.* 1971, ERICKSON 1973, WHITE 1971). Special searching and advertising behavior that facilitated reunion after separation would also promote continued association of partners (BUTTERFIELD 1970).

To exclude additional individuals from the bond once it is established, members must change their responses to unattached individuals. For example, a male ring dove's responses to his mate and to strange ♀♀ in a neutral area diverge progressively, a trend that continues even after the mates' first breeding cycle together (ERICKSON 1973). This change might normally depend on individual recognition of the partner but would not necessarily require it. The presence or behavior of a mated ♀ in his territory might lead a ♂ to react differently to a second ♀, regardless of an ability to recognize his mate individually. In some species, when the resident ♀ threatens newly arrived

♀♀, the resident ♂ joins in threatening the new ♀. Exclusion of additional individuals might also occur when a pair's activities, such as continually following each other, are incompatible with sustained interaction with other individuals.

Regulation of a pair's activity

Patterns in mates' interactions pose problems in the control of social dynamics, the changes in the state variables of a social structure, where the state variables are the locations and internal states of each individual at any moment. Social dynamics will often vary with differences in the partners' external circumstances and initial states. Over short time periods, social dynamics will include temporal and spatial coordination of the partners' actions, and over longer periods the seasonal progression of their internal states.

The interactions of tendencies to approach, attack and flee ultimately regulate the spatial relationship of partners (TINBERGEN 1953, 1959, HINDE 1955—56, MARLER 1956, MORRIS 1956). The waning of agonistic behavior between pair members allows closer association (TINBERGEN 1953, LAMPRECHT 1973). Spatial coordination in partners' movements is especially pronounced in species that form pairs in flocks before territories or nest sites are established. In these circumstances, mates often follow each other nearly continuously (LACK 1940, 1968). Temporal coordination of mates' behavior can also take striking forms, such as the duetting or antiphonal singing of some tropical birds with long-lasting pair bonds (THORPE 1972, PAYNE 1971, HOOKER and HOOKER 1969, DIAMOND and TERBORGH 1968, BERTRAM 1970, KUNKEL 1974) or the prolonged mutual display by heterosexual pairs of many birds and fish (HUXLEY 1914, NELSON 1965, BAERENDS and BAERENDS-VAN ROON 1950, BARLOW and GREEN 1970). Temporal coordination of partners' behavior often involves contagious reactions, tendencies to repeat the partners' preceding action. Emphasis on close temporal coordination of behavior seems likely to evolve when prompt individual identification or joint action by partners is especially important, as when pairs form before territories are established or when the pair engages in cooperative territorial defense.

Long-term changes in the interactions of paired individuals, over days or weeks, can depend both on cumulative effects of social interaction on the partners' internal states (LEHRMAN 1965, HINDE 1965, BROCKWAY 1969, NOTTEBOHM and NOTTEBOHM 1971) and on altered external circumstances, such as the construction of a nest (HINDE and WARREN 1959) or the presence of eggs and young (LEHRMAN 1965, HANSEN 1966). Although the progression of a pair's interactions will often involve concurrent changes in the partners' states, changes in the physiological states of only one partner can control the pair's interactions. For example, the increased gathering of nest material by male ring doves during the first week of the pair's association evidently depends on a change in the ♀'s hormonal state rather than the ♂'s (MARTINEZ-VARGAS and ERICKSON 1973).

The interactions among two partners and their external circumstances rarely if ever approach the ideal of a deterministic chain reaction (TINBERGEN 1951, MORRIS 1958, NELSON 1964). When interactions have cumulative effects on the partners' states, their response probabilities would change progressively over periods longer than the intervals between their reactions to each other. Relatively abrupt transitions would appear in the pair's interactions when a critical change occurred only after the cumulative effects of stimulation had reached a threshold.

Significance of variation in heterosexual interaction

In treating heterosexual affiliations of Common Grackles, I will give special consideration to variation among pairs in the partners' interactions and the seasonal course of their behavior. Comparisons of behavioral differences among pairs are in effect natural experiments, although generally it is not possible to control as many variables, by matching subjects, as in definitive experiments. Studies of variation in natural circumstances can none the less identify realistic hypotheses about behavioral mechanisms that could limit bond membership and control the seasonal progression of partners' interactions.

Procedures

For this study, I concentrated on one segment of a large colony that occupied several groves of pines on the grounds of the New York Zoological Society in Bronx Park, New York City. Because large numbers of people passed these trees every day, the birds were well habituated to human presence. By standing quietly at a distance of 10 to 15 m, I could observe the birds easily without their showing any signs of alarm. My observations began about sunrise and continued until shortly before 10:00 when the zoo opened. Activity decreased rapidly after the first 2—3 hours of daylight. Between 5 March and 26 May, I observed the colony on 41 mornings, with no absence longer than 7 days. 14 nests were built in a grove of 19 contiguous pines under regular observation. I intensively studied 4 pairs, G, B, D, and JJ, which differed strongly in the seasonal timing of breeding and the ♂'s fidelity to his mate.

Individual birds were identified by ear. Each individual ♂ and ♀ used one stereotyped song pattern (WILEY in press b). Although grackles were trapped near the colony and marked, I was not able to catch the intensively observed birds. Because ♀♀ sang less frequently after the start of incubation, I often had to identify ♀♀ later in the season by their association with their nest sites. I learned to recognize the songs of the eight ♂♂ that frequented the grove of pines in which all four of my regularly observed pairs nested. It took only a little practice before I could identify their songs whenever they sang in or near the colony. Although I made no systematic effort to learn the songs of other birds, I soon knew a number of these as well from their occasional visits to my primary study area.

Vocalizations and Action Patterns

Most of the vocalizations and distinctive action patterns recognized in the course of my study (WILEY in press b) could be identified with earlier descriptions by FICKEN (1963) and YANG and SELANDER (1968). Where my terminology differs from FICKEN'S, I have included his terms in parentheses.

Vocalizations

(1) Chack: a sharp, harsh call used by both sexes in many contexts, including during flight. (2) Chaa (Waa): a more prolonged, harsh call, most frequent among ♀♀, often during flight, most intensely during agonistic interactions. (3) Chitip: probably a variant of the Chaa, preferred by some ♀♀. (4) Brrrt (?Snarl): a brief call with nasal tonality, apparently restricted to ♂♂, often contagious among nearby ♂♂, not obviously associated with a particular context. (5) See (Peep): a high-pitched whistle accompanying both male and female precopulatory displays. (6) Song (Squeak; Chuga): a complex, stereotyped vocalization consisting of several noisy syllables and often a high-pitched whistle; one pattern per individual.

Distinctive action patterns

(1) Song-spread (Ruff-out): a variable coordination with ruffled contour feathers, spread wings and tail, and song. (2) Bill-up (Head-up): an upward rotation of the head, a threat display elicited by the close approach of another grackle. (3) Head-down: a coordination of erected contour feathers, spread wings and tail, downward flexion of the head, and alternating Song and See vocalizations; restricted to ♂♂ during close approaches to ♀♀; preceded most copulations. (4) Wing-quivering (Solicit): a display with widespread similarities among passerines; components included elevation of the tail, upward rotation

of the head, wing-quivering, and repeated See vocalizations; virtually restricted to ♀♀, usually prior to copulation.

Group Behavior Early in the Season

At winter roosts, Common Grackles showed no signs of heterosexual associations. The birds returning in long files to these roosts did not fly in pairs. As grackles gathered in the vicinity of their breeding colonies in early spring, two characteristic forms of group behavior occupied much of their time. In bare trees near the pine groves, birds of both sexes gathered to sing in closely spaced groups. About the same time, group flights, in which several ♂♂ and one or more ♀♀ participated, became a regular occurrence. From these two group activities the pairs eventually emerged. The contagious singing by perched groups and the group flights represented the precursors in group form of two characteristic interactions between paired birds: vocal answering, a form of antiphonal singing; and following.

Singing groups

Grackles appeared near their colonies, particularly on warm days, by the last week in February or the first in March. Characteristic of these early arrivals were closely spaced groups of 3—20 birds in the leafless hardwood trees near the pine groves. These groups, composed of both sexes, often clustered in one part of the tree's crown, each bird within 1 or 2 m of its neighbors. Such groups formed only occasionally in the pine groves, where the nests eventually were constructed.

Singing, the most frequent activity in these groups, was highly contagious. Often the whole group generated a confusing cacophony of overlapping songs, as each individual sang repeatedly.

3 or 4 birds sometimes sang repeatedly in the same sequence. The order of singing had no social significance that I could detect, as the sequence occasionally changed in the absence of any other interaction among the birds, and the order in which the sexes sang conformed to no rule. Single birds also sang in the leafless trees but usually not for long.

Grackles in these groups changed their positions in the tree infrequently and interacted with each other primarily by singing. Bill-up displays occurred particularly when a ♂ joining the group landed near another, but usually the two moved at least 1 m apart and ceased their Bill-ups. Occasionally a ♀ would wing-quiver briefly, usually without evoking a response. The restricted movements and interactions among the perched birds contrasted with the excitement of their arrivals and departures.

The composition of a singing group shifted continually, as small groups and single birds arrived and departed. Usually the group formed and disbanded entirely within a half hour. Often groups gathered in several different trees in the course of a morning, and sometimes two were in progress at once in nearby trees. Arriving ♂♂, alone or with other birds, flew with strongly keeled tails and sometimes sang in flight before landing. Arrivals usually sang soon after landing. Departing birds also flew singly or in small groups, the ♂♂ again with fully keeled tails.

Group flights

These performances, noted by almost every student of Common Grackles (FICKEN 1963, WIENS 1965, MAXWELL 1970) usually included one ♀ and 2 or more ♂♂. As FICKEN (1963) noted, ♂♂ occasionally lead. In Bronx Park,

among 78 group flights recorded between 5 and 26 March, the modal number of ♂♂ per flight was 3, slightly more than in those noted by FICKEN. The maximum number of ♂♂ in one flight was 7.

As in singing groups, the excitement of the participants in group flights varied markedly. Relatively leisurely flights with the ♀ leading occurred most frequently, though all variants occurred between fast, twisting chases and slow, almost fluttering flights. Fast flights usually occurred near tree-top level and included sudden dips by the leading ♀, accompanied by excited calling from all of the birds, as the ♂♂ bunched together and tried to track the ♀'s deviation.

Group flights were extensions of the activity in singing groups. When a ♀ left a singing group, usually several ♂♂ followed, particularly those perched near her. Normally only 2 or 3 ♂♂ would follow, leaving the remainder of the singing group behind. Once begun, group flights changed composition infrequently. Birds rarely left a group flight before it landed. Only once I observed a ♂ join a group flight as it passed his perch. In landing, a group flight might join a singing group or select an empty tree, where they might form the nucleus for a new singing group.

Pair formation

As pairs formed during these group activities, they concurrently shifted their activity to the pine groves. Pairs were only occasionally detected in the arrivals and departures from singing groups or in the initiations and terminations of group flights. One ♀ with an unusually distinctive song joined singing groups several times, the latest on March 18, the day after she had begun carrying nest material in association with a ♂.

As the season progressed, groups became smaller and shifted their activities to the pine groves, where definitive pair bonds matured. In my records, group flights that either originated from the pine groves or terminated there never included more than 2 ♂♂. The larger group flights started and ended in the bare trees in which singing groups usually congregated. Early in the season, on 5 and 6 March, both forms of group activity occurred regularly near the pine groves, but there were no indications of pairs. By 16 and 18 March pairs were seen regularly, while singing groups and group flights had become notably less frequent. After 22 March singing groups and group flights occurred only rarely, and pairs arrived and departed repeatedly from the pines.

Conspecific, heterosexual and individual specificity in the initial interactions

The pair bonds emerged from the ♂♂'s and ♀♀'s interactions with each other within group activities. The establishment of pair affiliations in groups of conspecific individuals should easily insure the limitation of bonds to conspecifics. All the species-specific morphological and vocal features are available with exhaustive redundancy to both sexes in such groups.

The heterosexual limitation of bonds in the Common Grackle occurs less obviously. The sexes differ only slightly in size and intensity of coloration. There are also several differences in vocalizations. ♀♀'s songs more often include high-frequency whistles than do ♂♂'s, although this difference is not absolute (WILEY in press b). ♂♂ also have a distinctive call, the Brtt, never recorded from a ♀. These vocal and plumage characters probably facilitate sex-specificity in individuals' responses.

The major forms of sex-limited behavior, however, are the tendencies of ♀♀ to lead group flights and ♂♂ to follow. This sexual difference continues during the pair's affiliation, when the ♀ usually, although not invariably, leads and the ♂ follows as the pair flies to and from the colony. As a sub-

sequent section will document, agonistic interactions contributed little to the sexual differentiation of behavior. The typical sexual roles of leading and following in flight, although perhaps ritualized derivations from agonistic behavior, had no definite connections with dominance and subordination.

The individual specificity of bonds evidently depended on a gradual development of individual recognition between individuals in singing groups. Because Common Grackles form pair bonds before localizing their activities around their future nest sites, individual identification independent of location is essential in their affiliations from the outset. Some pairs perhaps recognize each other from previous years and thus re-establish their affiliations more easily. Persistent association between two individuals in singing groups and during group flights, owing to the ♂'s tendencies to follow the ♀, could lead over days or weeks to individual recognition of each other's songs.

Once the ♀ shifts her activities to the groves and begins exploring, the pair is more isolated from close interaction with other birds. This shift may require that the ♀ have some prior familiarity with the songs of a particular ♂. The pairs then continue vocal answering through the first stages of their affiliation in the pine groves after they have separated from group activities, so the opportunities for learning individual characteristics continue. Vocal interaction between prospective mates over periods of days or weeks is probably the critical feature in the individuation of their responses to each other. The method of pair formation in this species seems directly related to the production of individually distinctive vocalizations by both sexes.

Seasonal Progression of a Pair's Affiliation

Introduction

Once a ♂ and ♀ began to associate regularly, their interaction during the rest of the nesting cycle developed gradually through 5 stages, delimited by 5 easily observed changes in the pair's behavior: the beginning of exploring behavior by the ♀, the localization of the ♀'s activity around a presumptive nest site, the completion of the nest cup, the onset of incubation, and the hatching of the eggs.

Stage I in a pair's association preceded the ♀'s selection of a nest site. During this period a ♀ exhibited characteristic exploring behavior, in which she hopped from perch to perch in a dense pine bough and periodically flew to a new location. Throughout this stage pairs regularly engaged in Song-answering, or "mutual display" (FICKEN 1963), a form of antiphonal singing in which a bird sings in answer to its mate's song. Each partner uses its own individual song type and each, on different occasions, answers the other's songs (WILEY in press a).

Localization of the pair's activities around a particular nest site inaugurated Stage II. Of 3 ♀♀ (G, D, JJ) studied through Stages I and II, 2 made the transition during a week when I was absent; a third made the change in 2 days. Some ♀♀ began building at two distinct sites before abandoning one of them, but usually a ♀ built at only one place. ♂♂ continued to follow their mates to and from the colony, and Song-answering also continued through Stage II.

Stage III began when the ♀ had completed the bulk of her nest. Usually, after 1 to 4 weeks of desultory building, which resulted in little progress on the nest, the ♀ finished most of the nest cup in one or two day's work. In 3 of the

intensively studied pairs, frequent copulation began 2 to 3 days later. Frequent trips for nest material characterized the first few days of Stage III. Eventually the ♀ began to bring fine grasses for the lining and then nest-building subsided to an infrequent activity. Throughout this stage Song-answering was infrequent, in contrast to earlier stages (WILEY in press a). The ♂ continued to follow his mate on most of her flights.

The onset of incubation initiated Stage IV. The ♂, now singing more sporadically, often perched in the colony near his incubating mate. The pair rarely answered each other's songs. The ♀'s long periods on the nest placed a constraint on the pair's tendency to remain together. After resting and preening for some time, the ♂ often left his mate alone. On occasion, she would leave first and he would follow her. Often, though, the ♀ left while her mate was away.

Stage V began when the eggs hatched. Of the 4 intensively studied pairs, 3 reached this stage during my study. ♀ JJ's eggs had not yet hatched on the last day of observations. Pair D's nest was wrecked during a day of heavy rain shortly after hatching. Brooding, like incubation, was performed solely by the ♀.

Differences among pairs in the duration of the partners' association

The ♂'s attendance near the nest during incubation followed different patterns in the 4 intensively studied pairs. ♂ G remained in attendance throughout incubation, although he became progressively quieter. ♂ D spent progressively less time in the colony, although even toward the end of incubation he still visited regularly. ♂ B, in contrast, made his last appearance near his mate's nest within a week after the first day of incubation. ♂ JJ likewise disappeared before the middle of incubation.

Of 2 other pairs whose progress was followed daily in this colony, the ♂♂ also deserted quickly after the start of incubation. One of these, ♂ O, like ♂ B, was subsequently seen only rarely. The other, ♂ Z, 5 days after his mate began to incubate, had a second mate already actively building a nest 15 m away from his first mate's nest. ♂ Z never subsequently approached or interacted with his former mate. As ♂♂ B and O never returned to their mates, even after their eggs had hatched, they too might have found second partners. They were known to have survived, because both later visited my area of observation and sang for a while before moving on.

♂♂ in this colony thus differed widely in their attachments to their mates: some remained attentive throughout incubation and nestling care; others deserted within a week after the start of incubation. The fact that ♂ D's attention waned, although not fast enough to result in desertion before the end of incubation, suggests that the changes in a ♂'s attentiveness during incubation vary between the two extremes exemplified by ♂♂ G and B (WILEY in press a). While some ♂♂ remained monogamous, others practiced sequential polygyny.

Both sexes fed the nestlings, provided the ♂ had remained with his mate through incubation. ♀ B, whose mate had long ago deserted her, fed her nestlings alone beginning on 21 May. Another deserted ♀, O, also fed her nestlings alone, beginning on 7 May. In other pairs, like Pair G, whose eggs hatched between 14 and 19 May, both partners fed the young. The ♂♂'s alternative strategies of desertion or fidelity persisted through brood care. No ♂ returned to help feed his mate's nestlings after he had deserted during incubation.

♂ G fed the nestlings more frequently than did his mate. On the morning of 19 May he brought food 7 times in 1.5 hours and remained at the nest less than 1 min each time. On subsequent mornings his feeding rate decreased

and he spent longer periods near the nest. His mate at first spent long periods brooding but also brought food regularly. On four mornings between 19 and 26 May, ♂ G averaged 4.1 trips per hour and his mate 3.1 trips per hour.

♀ B, deserted by her mate, fed her nestlings alone. On the first morning she made 3.6 trips per hour (1.7 hours of observation), but later increased her rate. On 3 mornings between 21 and 26 May she averaged 4.3 trips per hour. These figures, although too few for definite conclusions, suggest that ♀ B, deserted by her mate, fed her nestlings more frequently than did ♀ G, aided by her mate, but not so frequently as the combined rate for the pair. ♀ O, also deserted by her mate, brought food less frequently than ♀ B: 3.0 times per hour during the first 4 days after hatching (4 hours of observation). ♀♀ B and O tended to collect food closer to the colony than did Pair G, often within 50 m of their nests, while both partners of Pair G usually arrived from at least 100 m away. In providing for the young, these two ♀♀ seem to have compensated only partially for the absence of their mates.

Variation in the sequence of activities during the early stages of the nesting cycle

A pair's behavior did not proceed evenly through the stages of the breeding cycle. Instead, several relatively abrupt transitions in the pair's behavior marked this progression. Two such transitions involved changes in the ♀'s behavior, accompanied or followed immediately by the first appearance of a consummatory behavior pattern. Thus localization at a nest site normally coincided with the first nest-building, although collection of nest material occurred earlier. Then the ♀'s rapid completion of the nest some days or weeks later brought the virtual cessation of vocal answering and the onset of copulation, although the ♂ had performed Head-down precopulatory displays earlier. Two subsequent transitions coincided with ovulation and hatching of the eggs.

Variation among pairs appeared in the timing of these transitions, the frequencies of different activities, and the sequence in which activities first appeared. The differences in the faithfulness of the ♂♂ in different pairs are foreshadowed as early as Stage II of their affiliations. Fig. 1 documents for the 4 intensively studied pairs the seasonal occurrence of exploring, localization of the ♀'s activity at a prospective nest site, carrying nest material, and the appearance of a substantially completed nest.

Exploration: Exploring was the first activity performed in the nesting trees by pairs. Some ♀♀ evidently began exploring in the pines before they had found mates, as on several occasions ♀♀ investigated pine boughs without any ♂ in attendance. On the other hand, an exploring ♀ was once accompanied by two ♂♂, although neither followed her when she flew away. Normally, an exploring ♀ had a mate perched within 3 m that immediately followed whenever she flew any appreciable distance.

Some pairs selected a nest site quickly and consequently manifested little or no exploring behavior. Others prolonged this stage for over a week. ♀♀ JJ and B provided a strong contrast in this respect. From the day of her first appearance on 12 March, ♀ B localized her activities to a particular place in one tree. She first carried nest material there on her first day in association with ♂ B, who had sung conspicuously around the colony for several days previously. This ♀ was never seen exploring.

Pair JJ, when first noted on 12 April, engaged in frequent antiphonal singing while the ♀ spent long periods exploring in several trees in the colony. For the next 10 days, the ♀ continued to explore in different trees, the two partners frequently sang antiphonally, and the ♂ closely followed the ♀ when

Date	Pair B				Pair G				Pair D				Pair JJ			
	Ex	Nm	Cp	I/F	Ex	Nm	Cp	I/F	Ex	Nm	Cp	I/F	Ex	Nm	Cp	I/F
March 31	e,L				e	n										
April 2					e	n			e							
5		n			e	n			e							
12					L	N			e,L	n			e			
13						n							e			
14									n							
15		n				n										
16									n				e	n		
19		n							N,S				e	n		
20						n			n				e			
22		n				N				c			e(L)	N		
23										c				n		
26						N,S				c			e	n		
27		N				N	c				I		N			
29		N,S											e			
30		n					c								c	
May 4								I					L	n,S		
5			I											n		
7														n	c	
10														n	c	
14			♂Ab								F					I
17								F								
19									n							
21			F						N							♂Ab
24										c						
26											I					

Fig. 1: Seasonal progression of breeding activities by 4 pairs of Common Grackles. Activities are recorded as follows: e, exploring by the ♀; L, first morning that the ♀ localized her activities in the colony at a presumptive nest site; (L), temporary localization, not persisting on following days (Pair JJ only); n and N, nest material carried by the ♀ less than (n) or more than (N) 4 times per hour; S, first morning on which the nest cup was substantially completed; c, copulation; I, incubation; F, feeding of nestlings; ♂Ab, day on which the ♂'s absence from association with his mate became continuous (Pairs B and JJ only). Horizontal lines indicate days on which the pair did not serve as subjects for timed observations. On these days, a pair was observed less systematically. Nevertheless, because they all nested within 20 m of each other, I obtained some information about each pair every day of observation

she flew. During this time they investigated different places within a diameter of 15 m in at least 5 trees. On 22 April the ♀ preferred a site in one of these trees, where she carried nest material a number of times to a flimsy ring, the beginning of a nest. However, her interest in this nest site waned until, on

29 and 30 April, she hardly visited it and instead explored in several trees nearby. Finally, on 4 May, after a three-day absence of mine, she had completed the major portion of a nest located 3 m from her earlier site in the same tree. ♀ JJ, after an initial 10 days or more of exploring, first localized her activity at one site, gradually relapsed to exploring over a period of 8 days, then suddenly picked a new site nearby and constructed most of her nest in less than 4 days.

♀♀ G and D both showed intermediate persistence in their exploring. ♀ D was first observed exploring on 23 March, about 20 days before she localized her activities to one site. ♀ G began exploring as early as 26 March; like ♀ D she had localized her activities by 12 April. Each remained attached to her first nest site. ♀ D showed some interest in a second site on 16 April, but soon confined her attentions to her original site; ♀ G, once localized, never carried nest material or explored in other places. The behavior of ♀♀ G and D was more typical than that of ♀♀ B and JJ. Other pairs in the colony, although observed less systematically, engaged in 10–20 days of exploring and then settled at a permanent nest site.

♀ B and ♀ G thus chose nest sites and stuck to them without further exploring. ♀ D temporarily showed some interest in a second site. Only ♀ JJ changed sites.

Collection of nest material: The first ♀ was seen with nest material on 9 March. None carried nest material regularly until 30 March, when ♀ Y repeatedly brought material to her newly chosen nest site.

♀♀ occasionally carried strands of nest material before they had chosen a nest site, while they were still exploring. ♀♀ G and JJ began collecting nest material at least 12 and 6 days, respectively, before they chose nest sites. On the other hand, ♀ D did not collect material until the first day that she localized her activities. Once a ♀ chose a site, she collected nest material more often than previously, although this increase usually did not persist. Only during Stage III, when she began the final surge of activity that resulted within a few days in a substantially completed nest cup, did a ♀ collect material at maximum rates, as often as 9 times in a half hour.

Nest-building: Nest-building normally began only after localization at a nest site. ♀ JJ, the only exception among the 4 carefully studied pairs, briefly performed nest-building actions 3 and 9 days before localization, perhaps because she chose her nest site so much later in the season than did the other 3 ♀♀.

Nest construction proceeded unevenly for every regularly observed pair, a situation other observers have also noted (PETERSEN and YOUNG 1950; MAXWELL 1970). For a variable period of 5–25 days after the ♀'s choice of a nest site, little progress was made on the nest; day after day it consisted of little more than a frail ring or platform. Then within 3 days the ♀ essentially finished the outer shell of the nest, all except the lining. ♀♀ that chose a nest site earlier in the season usually delayed the final surge of nest-building longer than those that chose nest sites later, so that temporal variation in the completion of nests was less than that in the choice of nest sites.

Nest-building was normally performed only by the ♀. ♂ D, the only ♂ observed nest-building, began to build after his mate's first nest had been damaged by a storm just after hatching. ♂ D seemed ready to reneest sooner than his mate. In this circumstance, the ♂ performed nest-building and collected nest material a number of times over a period of at least 3 days. At first his mate showed little interest in the damaged nest and only visited the colony for relatively short periods, but by 21 May the ♀ was collecting material and

building regularly. Once the ♀ herself began reconstructing the nest, the ♂ ceased this work. Once earlier, on 12 April, the first day that his mate localized her activity at one site, ♂ D had picked up nest material from the ground but did not carry it. Normally a ♂ took only an indirect part in nest construction, through whatever stimulation his behavior might have provided for the ♀'s tendencies to build.

Copulation and Head-down displays: During the first one or two days of Stage III the ♀ worked assiduously on the nest, but thereafter her trips for nest material and her bouts of nest-building became much less frequent. Each pair first copulated one to three days after the first substantial progress on the nest, with the exception of Pair JJ, the last of the regularly studied pairs to enter Stage III; they copulated once shortly before the ♀ had constructed the bulk of her nest. Copulation thus was normally restricted to the last part of Stage III after the bulk of the nest had been completed.

Head-down displays by the ♂, on the other hand, appeared earlier in the pair's association. ♂♂ B, D, and JJ performed Head-down displays to their mates at least 14, 2 and 1 days before Stage III, while ♂ G was first recorded performing Head-down displays to his mate on 2 April, at least 22 days before Stage III began. In the following two weeks ♂ G performed this display to his mate on 8 recorded occasions. None, however, was observed in the 9–11 days immediately preceding Stage III. During the latter part of Stage III, when copulations occurred regularly, ♂♂ frequently addressed Head-down displays to their mates. At least 3 per hour were recorded for ♂♂ G, D, and JJ on one morning during Stage III.

Some ♂♂ occasionally directed Head-down displays to ♀♀ other than their mates. 3 ♂♂, B, JJ, and Z, known to have eventually deserted their mates, displayed to other ♀♀ even before terminating their bonds with their mates. ♂♂ G and D, known to have remained faithful to their mates, in contrast, never displayed to other ♀♀ during my observations.

All Head-down displays outside the pair bond were addressed to incubating ♀♀, usually ♀♀ in the first few days of incubation. Thus ♂ B performed Head-downs and closely approached ♀ O on her nest on 20 and 22 April; also ♂ JJ displayed to this ♀ on the 22nd. ♂ Z behaved similarly to ♀ D on her nest on 27 April before his mate had made much progress on her nest. Then on 4 occasions on 14 May, ♂ Z displayed to ♀♀ D and JJ on their nests, while his mate worked persistently on her nearly completed nest. On one occasion he briefly mounted ♀ D while she incubated. Twice he clearly performed a display typical of ♀♀, Wing-quivering, at a distance from any other bird, before flying to approach a ♀ in an adjoining tree. After his mate had begun incubation, ♂ Z once approached ♀ W, also just beginning to incubate. Although Head-down displays were the most frequent way a paired ♂ interacted with another ♀, on 26 March ♂ B once engaged in a bout of Song-answering with a ♀ not his mate. Thus those ♂♂ that eventually deserted their mates during incubation had already interacted earlier with ♀♀ other than their mates.

The Varieties of Agonistic Behavior

The circumstances in which aggression occurred suggest that aggression had a minor part in establishing or maintaining the individual specificity of pair bonds. Throughout the season, aggression ordinarily resulted either from unusual proximity between individuals or defense of a nest site.

Kinds of agonistic behavior observed in this study included Bill-up displays; supplantations, in which one bird withdrew as another approached; pecking; and rarely, direct attacks and grappling fights. A frequent form of aggression involved a ♀ defending her nest from close approach by another ♀, as previous observers have noted (FICKEN 1963, MAXWELL 1970). However, both sexes were at times aggressive to individuals of the opposite sex as well as to members of their own sex.

Agonistic interactions with birds other than the mate

Aggression toward birds other than the aggressor's mate fell into 4 categories: (1) Bill-up displays or supplantations by one or both birds after one had approached the other within 1—2 m; (2) similar behavior after another grackle had approached the aggressor's mate within 1—2 m; (3) attack directed at a copulating pair; and (4) supplantation or attack when another bird closely approached the nest site.

Abrupt close approach by a ♂ occurred most frequently early in the season before pairs had formed, as described earlier. A ♂ landing in a singing group often evoked Bill-up displays from nearby ♂♂ and occasionally from a nearby ♀. The new arrival often performed Bill-up threats in return. Although the most frequent situation early in the season involved threat displays by ♂♂ after another ♂ had landed nearby, both sexes at times performed Bill-up displays after approaching a ♂ or after a ♂ had approached closely.

Early in the season, therefore, aggression occurred primarily as a result of close proximity to another individual. Later in the season, after pairs had formed, nearly all agonistic interactions with individuals other than the actor's mate occurred near the actor's nest site or mate. In the pine groves used for nesting, close, abrupt approaches rarely occurred among unmated birds.

♂♂ only occasionally displaced other ♂♂ near their mates, and only two such instances involved an approaching ♂ not accompanied by his own mate. On one occasion ♂ O displaced ♂ B, while the latter performed Head-down displays to ♀ O as she incubated. Twice on the ground near the colony a paired ♂ displaced another ♂ that approached within 1 m of his mate. These interactions between paired and single ♂♂ occurred so rarely in part because single ♂♂ rarely approached pairs.

One ♂ displaced others from near one or two ♀♀ on 4 occasions during March. On these occasions early in the season the displaced ♂♂ sometimes stayed nearby and followed the ♀ when she flew. These interactions might therefore represent an early stage in pair formation, when more than one ♂ still vied for the same ♀. Twice in March two ♂♂ fought each other, grappling in mid-air as they tumbled to the ground. The circumstances leading to these fights were not observed. The infrequency and the usual brevity of interactions between paired or single ♂♂ suggested that aggression between ♂♂ played a subsidiary role in the formation and maintenance of pair bonds.

A paired ♂ sometimes approached and seconded his mate during her attempts to displace other ♀♀ from near her nest. Before the ♂ approached in these situations, his mate either supplanted or was supplanted by the other ♀. Both of the ♀♀ involved usually had nearby mates. In these situations the ♂ often displaced the opposing ♀, rather than the ♂. His aggression toward the opposing ♀ might have stemmed from her interaction with his mate, from her position closer to his mate or the presumptive nest site, or from redirected aggression evoked by the opposing ♂. These encounters sometimes erupted into overt fighting. In 7 of 12 interactions between paired ♀♀ in which at least one of the ♂♂ approached, the interaction resulted in a scuffle among all 4

birds. In a few cases, the ♀♀'s scolds attracted other grackles and generated a commotion among the excited grackles.

A third category of aggression between unpaired birds includes instances in which a ♂ attacked a copulating pair. In the 5 cases observed, the attack immediately interrupted the copulation. The copulating ♂ proceeded to supplant the attacker repeatedly until the latter left. The ♀ meanwhile often continued to wing-quiver. The copulation was then resumed after the attacker had departed.

Agonistic encounters near a nest

In the most frequent form of aggression between grackles, one ♀ displaced another ♀ from near her nest site, behavior recorded for each of the intensively studied pairs. Usually the intruding ♀ came within 1 m of the nest site before evoking attack. However, ♀ G during Stage II diligently defended an area in the tree (N4) adjacent to the tree containing her nest site (N6). She had explored in N4 on several days before choosing her nest site in N6, and she seemed to maintain her proprietary interest in the part of N4 nearest her nest site. She engaged in vigorous disputes with ♀ JJ, who explored in N4 after ♀ G had settled in N6. After 20 April, ♀ G temporarily ceased trying to defend N4. A month later, though, after her eggs had hatched, she once again defended the west side of this tree against ♀ WH, who explored there. No other ♀ consistently defended more than 1 m around her nest.

During incubation a ♀'s defense of her nest site slackened. On two occasions, grackles approached incubating ♀♀ within 1 m without evoking a response. Some incubating ♀♀ did respond, though. Once during Stage IV ♀ D pecked another ♀ beside her nest, and once she displaced a nearby ♀.

♂ D, more than the other ♂♂ observed, helped in the defense of his mate's nest site. On 6 occasions he displaced ♀♀ near the nest site and once displaced the intruding ♀'s mate as well. A single ♂ was displaced from near the nest site on another occasion. Two of these instances occurred after the nest had been damaged during a storm; all other instances occurred during Stages III and IV. Another ♂, Y, also once displaced an intruding ♀ from near his mate's nest. In all of these cases the ♂'s mate was absent at the time. None of the other intensively studied ♂♂ helped to defend their mate's nest.

The importance of defending the nest became clear on several occasions when ♀♀ visited a neighboring nest to steal material in the owner's absence. For instance, on 22 April ♀ B stole material from ♀ G's nest in an adjoining tree. ♀ D's nest was robbed on two widely separated days during my observations, both on days when ♀ D was absent for long periods.

Thus, aggression with reference to a particular location, although rudimentary, appeared in both sexes. Once the ♀ localized her activities to a presumptive nest site, she began to defend, with some lapses, an area a few m in diameter around this site. The ♂ participated in defense of the nest site less than his mate, but he often joined the encounter when his mate faced an intruding pair.

Agonistic interactions between paired birds

Aggression between paired birds took one form: a presumably unreceptive ♀ would peck her mate as he approached closely in Head-down display. Head-down display occurred most commonly during Stage III, when the pair copulated often (see above). In contrast, the two observed instances of the ♀ pecking her mate during Head-down display occurred at times when copulation

was unlikely, once in the middle of Stage II (Pair G) and once on the last day of Stage III (Pair D).

On a few occasions ♂♂ attacked ♀♀ in situations that seemed related to pair formation rather than nest defense. Twice early in the season single ♂♂ attacked ♀♀ in the pines without evident provocation and then chased them. On another occasion in March my attention was caught by a ♂ and a ♀ that fell from a pine tree grappling in an outright fight. The ♂ then pursued the ♀ to a nearby tree where he performed Head-down displays, she wing-quivered, and both sang. Soon the ♀ flew back to the pines with the ♂ following. This ♀, E, had carried nest material the day before. Although the evidence is only suggestive, the interactions of ♂♂ and ♀♀ early in the process of pair formation seem to erupt on occasion into outright fighting.

Agonistic behavior thus seemed not to play any consistent part in the restriction of bond formation to birds of opposite sex, as sex-limited threat and submission were almost absent from the early interactions of prospective mates. In this respect, pair formation in this species differed from BAERENDS and BAERENDS-VAN ROON's (1950) model for pair formation in monogamous cichlids or TINBERGEN's (1953) description of pair formation in gulls.

Agonistic behavior and the individual specificity of bonds

In the early stages of pair formation by Common Grackles, aggression between ♂♂ near a ♀ suggested that competition among ♂♂ for positions close to prospective mates did occasionally occur before the individual specificity of bonds was well established. Even so, the ♂'s persistent attendance and vocal interaction were probably more important in establishing the individual specificity of the affiliation.

Later in the pairs' affiliations, ♂♂ defended their mates from other ♂♂ when the pair was attacked during copulation. Otherwise, the ♂'s aggression did not play a large part in maintaining the exclusiveness of the pair's affiliation. Instead, while the bond continued, both members of the pair restricted their affiliational responses, including following and antiphonal singing, to each other, and other individuals largely avoided attempts to intrude into these activities. The continuity of the pair's association largely insured the exclusiveness of their bond.

Aggression and proximity

Most agonistic behavior among Common Grackles resulted from unusual proximity between individuals. Thus early in the season Bill-up displays often followed a ♂'s arrival in a singing group near other ♂♂. In similar circumstances, ♀♀ also sometimes responded with Bill-ups. ♀♀ early in the season occasionally displayed a form of submissive behavior, Wing-quivering, when a ♂ suddenly landed nearby. Between mates the rare instances of agonistic behavior by the ♀ usually resulted from the ♂'s close approach in Head-down display at a time when she was unreceptive, either during Stage I or II or immediately following copulation. Although mates stayed near each other almost continuously through Stage III, unusually close proximity of the partner evoked momentary aggression or avoidance. Between unmated individuals, whether of the same or opposite sex, somewhat greater separations between individuals resulted in agonistic responses. The spatial separation between partners varied around a characteristic average distance of one to two meters, as a result of agonistic responses at very short distances and approach or following responses at longer distances.

Comparisons with Pair Affiliation in a Related Species

The heterosexual behavior of Common Grackles observed in this study closely resembles that of the related Brewer's Blackbird, *Euphagus cyanocephalus* (WILLIAMS 1952, HORN 1968, 1970). WILLIAMS in particular describes the regular occurrence of antiphonal vocalizations and chases during pair formation. WILLIAMS only mentions the ♀ responding to the ♂'s songs, while both sexes of Common Grackles answer each other. Both WILLIAMS and HORN observe that chases often begin when the ♂ darts toward the ♀, while in Common Grackles group flights almost always begin with the ♀'s departure rather than with a ♂'s advance. Threats between ♂♂ seem more frequent in Brewer's Blackbirds and often occur when one ♂ approaches another's mate. Defense of the ♀ by her mate might thus play a larger part in maintaining the exclusiveness of the pair's affiliation.

HORN (1970) describes in some detail the attraction of nearby ♂♂ to ♀♀ performing precopulatory displays (similar to the ♀ Common Grackle's Wing-quivering). The resultant agonistic interactions between these ♂♂ and the ♀'s mate sometimes culminate in all of the ♂♂ chasing the one ♀. The ♀'s precopulatory display is highly contagious, and ♂♂ perform a similar display which also stimulates precopulatory displays in nearby ♀♀. Among Common Grackles, in contrast, the ♂'s precopulatory display, the Head-down, differs markedly from the ♀'s Wing-quivering, and neither display has much effect on individuals other than the mate. Copulation itself often evokes an attack by a nearby ♂ and consequently agonistic interactions between the two ♂♂, but in my observations group flights never resulted. Both ♂ and ♀ precopulatory displays occurred predominantly in the days prior to egg-laying and clearly had little effect on the maintenance of the affiliation through the weeks of Stages I and II.

In Brewer's Blackbirds, WILLIAMS reports, ♂♂ often leave their first mates during incubation and take second mates. As in the case of ♂ ZZ in my study, the second affiliation lacks the prolonged stages prior to intensive nest-building. Unlike the ♂♂ in my study, however, bigamous male Brewer's Blackbirds normally return to help their first mate feed her young. The restriction of affiliation to two individuals at a time resembles the situation in Common Grackles.

Comparisons Among Pairs of Common Grackles

The 4 intensively studied pairs differed in the pacing of their nesting cycles and in the faithfulness of the ♂. The first sort of variation primarily concerned the long-term changes in the ♀'s activities prior to intensive nest-building, while the second sort of variation primarily concerned the ♂'s behavior and hardly appeared before the start of incubation.

Seasonal pacing

The ♀♀ I studied differed strongly in how quickly they localized their activities at prospective nest sites. ♀ B, for instance, settled at her nest site almost immediately although she did not finish her nest until nearly a month later; in contrast ♀ JJ explored persistently, changed from one site to another, and finally settled on her final site and completed most of her nest within 5 days. Other ♀♀ in the colony chose their nest sites both earlier and later in the season than did ♀♀ B and JJ.

Regardless of the timing of Stages I and II, the ♀♀ showed considerable variation in their activities during these early stages. The frequencies of nest-building and collecting material waxed and waned. Although building generally occurred only after localization, collecting material began while some ♀♀ were still exploring.

The rapid completion of the bulk of the nest coincided with a change in the pacing of the pair's interactions. Preceding this transition, marking the start of Stage III, the durations and sequence of events varied considerably. After this point, the activities of Stage III, leading to incubation, progressed on a much more regular schedule. The transition in the ♀'s behavior that resulted in a sudden increase in her building activity was then critical in the pacing of the pair's behavior.

This transition in the ♀'s state might have depended on tonic stimulation from the pair's strongly coordinated behavior during Stages I and II (WILEY in press a). The ♂'s behavior is known to facilitate the ♀'s nest-building in several species of birds: ring dove (LEHRMAN 1965; ERICKSON and LEHRMAN 1964); canary (HINDE 1965); budgerigar (BROCKWAY 1967, 1969). These species, like grackles, nest in loose colonies, show weak territoriality, and form durable heterosexual affiliations. When tonic stimulation by a mate is important for seasonal reproductive development, pair formation must normally take place well before nest-building or egg-laying.

The rapid establishment of a second affiliation by bigamous ♂♂, like ♂ ZZ or WILLIAMS' (1952) Brewer's Blackbirds, poses an unsolved problem. Their late pair formation should entail much weaker affiliation between the partners. The ♀'s transition to Stage III, intensive nest-building, must occur without prior substantial association with a male partner, but might derive some stimulation from the behavior of other pairs. At the other extreme, ♀ JJ delayed localization at a nest site and intensive building in spite of intense, prolonged interaction with her mate (see also WILEY in press a).

In both cases, the behavior of ♀♀ that built their nests later in the season seemed relatively less dependent on interactions with mates. The later nesting ♀♀, by analogy with other passerines, might have included the inexperienced, first-year individuals (see WILEY in press a).

Desertion and loyalty of ♂♂: the persistence of the affiliation

Frequent desertion by ♂♂ during incubation and successive bigamy are not reported in previous studies of the Common Grackle (PETERSEN and YOUNG 1950; FICKEN 1963; WIENS 1965; SNELLING 1968; MAXWELL 1970). About half of the ♂♂ in the colony that I watched deserted their mates during incubation. At the only two such nests that hatched during my study the ♂ did not return to help feed the nestlings. The other half of the ♂♂ remained with their mates through incubation and took a major part in feeding the young.

Among the four intensively studied pairs, the ♂♂ that eventually deserted had already displayed occasionally to other ♀♀ prior to Stage III. On the other hand, ♂♂'s interactions with their mates, in particular the length of the pair's association in the colony prior to intensive nest-building, did not differ consistently between loyal and deserting ♂♂.

After egg-laying the maintenance of the affiliation might have depended on differences in the ♀♀'s reactions to their mates or on differences inherent in the ♂♂. The early appearance of interactions with other ♀♀ in those ♂♂ that eventually deserted suggests that the ♂♂ themselves did differ in their ten-

dencies to continue the affiliation. More detailed analysis of the pair's vocal interactions (WILEY in press a) reveals that one of the deserted ♀♀ responded to her mate less frequently both before and after egg-laying.

The Adaptive Significance of the Long Association Prior to Ovulation

If the ♂'s aid in feeding nestlings contributes appreciably to the ♀'s nesting success, it might prove advantageous for the ♀ to lay eggs only after relatively long association with her mate. As TRIVERS (1972) has pointed out, whenever one partner's investment in the breeding effort substantially exceeds the other's, the one with the lesser commitment might increase its reproductive rate by deserting and taking a second mate. When nest-building and laying by the ♀ are conditional on long previous association with the ♂, then the ♀'s commitment in time and egg production is partially offset by a substantial commitment of the ♂'s time. Thus a requirement for relatively prolonged involvement of the ♂ in the reproductive development of the ♀ might evolve to increase the chances that the ♂ would remain faithful to his mate. In species in which the ♂ is committed to a territory before the ♀ arrives, this commitment might help to insure the ♂'s fidelity to his mate without long prior association. Weak territoriality, as exhibited by Common Grackles, should thus favor the evolution of a long association between mates prior to ovulation for two reasons: ♀♀ could partially protect themselves from desertion by increasing the ♂'s commitment of time; and the absence of a common attachment to a territory would require more definite individual recognition for the continuation of the bond.

In the absence of data on nesting success, I cannot assess the adaptedness of the alternative strategies of desertion and fidelity among ♂ Common Grackles in Bronx Park. Possibly the abundant food available here for an omnivorous species, like the Common Grackle, has reduced the advantage of dual parental care. If so, the nesting success of ♀♀ with and without help from a ♂ would differ little, and the advantage of monogamy for either a ♂ or a ♀ would decrease. If the coexistence of alternative strategies in heterosexual affiliations is a stable feature of this population, the selection pressures that might maintain this behavioral diversity would depend on the genetic and developmental bases for the differences in behavior. If these differences correlated with genetic differences among individuals, a form of frequency dependent or diversifying selection might explain the persistence of different behavioral phenotypes (DOBZHANSKY 1970). If the behavioral differences correlated with age, one would have to identify selection pressures responsible for the corresponding life-history parameters of individuals in this population (see WILEY 1974 a, b).

Acknowledgments

The field work, aided by a grant from Sigma Xi, was conducted while I held a NIH postdoctoral traineeship (GM 1789) at The Rockefeller University. Analysis of the data was supported by grant MH 22316 from the National Institute of Mental Health. MINNA S. WILEY and SUE A. HARTNETT provided indispensable help with the analyses, and Ms. HARTNETT helped in preparing the figure. Stimulating discussions with Peter MARLER and his associates at The Rockefeller University contributed greatly to this study. Dr. GUNDA RIEGER kindly prepared the German summary.

Summary

Heterosexual affiliations require conspecific, heterosexual, and individual specificity in partners' responses. The individual specificity of the bond in turn requires both the exclusion of additional individuals from membership in the bond and the maintenance of continuity in the partners' association with each other. This study examines these forms of specificity in the pair affiliations of Common Grackles (*Quiscalus quiscula*, Icteridae). I could recognize individual ♂♂ and ♀♀ by ear by their distinctive songs. Pair bonds formed during group activities prior to the ♀'s localization at a nest site. Two characteristic activities of pairs, following and vocal answering, developed from two forms of group activity, group flights and group singing. In this species, the individual specificity of an affiliation involves primarily the partners' tendencies to restrict their following and vocal answering to each other.

In contrast to studies by previous authors, about half of the ♂♂ in my study area deserted their mates during incubation. Most of these ♂♂ left the immediate vicinity, although some of them continued to visit. None, after deserting, returned to help their mates feed the nestlings. One ♂, after deserting his first mate, took a second within 5 days. Other ♂♂ under study remained faithful to their mates and helped to feed the young. Only ♂♂ that eventually deserted their mates interacted with other ♀♀ before their first mate had finished building her nest.

The seasonal progression of a pair's activity exhibited considerable variability during the stages prior to the completion of the nest. The onset of intensive nest building by the ♀ marked the beginning of a more regular progression through the subsequent stages of copulation and incubation. The 4 intensively studied pairs differed considerably in the seasonal progression of their behavior, particularly the date on which the ♀ first localized her activity at a prospective nest site.

The contexts of aggression among grackles in their breeding colonies suggest that agonistic interactions serve primarily to adjust the spatial relationships of individuals, both between partners and between unpaired birds. Locality dependent aggression occurs in both sexes, but especially ♀♀, and only in the immediate vicinity of the nest. Agonistic interaction, even of low intensity, is extremely rare between partners and probably does not explain sexual differences in behavior. Intrasexual agonistic interaction probably has little role in maintaining the exclusiveness of the pair affiliations, although low intensity threat might influence the initial stages of pair formation during group activities.

Zusammenfassung

Heterosexuelle Bindungen erfordern art-, geschlechts- und individuentypische Reaktionen der Partner aufeinander. Nötig ist ferner der Ausschluß weiterer Individuen sowie das Erhalten der Partnerbindung. Die vorliegende Studie untersucht dieses Verhalten bei *Quiscalus quiscula* (Icteridae). Die einzelnen ♂♂ und ♀♀ konnte ich am Gesang unterscheiden. Die Paarbildung erfolgte während Gruppenaktivitäten, bevor das ♀ einen Nistplatz wählte. Zwei für Paare charakteristische Verhaltensweisen, das Folgen und der Antwort-Gesang, entwickelten sich dabei aus zwei Formen des Gruppenverhaltens, den Gruppenflügen und dem Gruppengesang. Die individuelle Spezifität einer

Bindung hängt vor allem von der Tendenz der Partner ab, ihr Folgen und ihren Antwort-Gesang aufeinander zu beschränken.

Im Gegensatz zu Untersuchungen anderer Autoren verließen etwa die Hälfte der ♂♂ in meinem Untersuchungsgebiet ihre ♀♀ während des Brütens, die meisten ♂♂ verließen auch die nähere Umgebung, einige besuchten den Platz jedoch immer wieder. Keines dieser ♂♂ kehrte zurück, um dem ♀ beim Füttern zu helfen. Ein ♂ wählte ein zweites ♀ innerhalb von 5 Tagen. Andere ♂♂ blieben jedoch beim ♀ und halfen beim Füttern. Nur die ♂♂, die ihr ♀ schließlich verließen, verbanden sich mit einem anderen ♀, bevor das erste sein Nest fertiggebaut hatte.

Das Verhalten der Paare vor der groben Fertigstellung des Nestes variiert beträchtlich. Der Beginn intensiven Nestbaus des ♀ war auch der Beginn eines geregelteren Verhaltens des Pärchens, was die folgenden Stadien der Kopulation und des Brütens kennzeichnete.

Kampfverhalten scheint vornehmlich der Regulierung der räumlichen Beziehungen der Individuen, sowohl zwischen den Partnern eines Pärchens, als auch zwischen einzelnen Vögeln zu dienen. Kampfverhalten auch mit sehr geringer Intensität tritt zwischen Partnern äußerst selten auf und erklärt wahrscheinlich nicht sexuelle Verhaltensunterschiede. Kampfverhalten gegen Gleichgeschlechtliche spielte für das Aufrechterhalten der Verbindung eines Paares wahrscheinlich eine geringe Rolle, obwohl Drohungen mit geringer Intensität während Gruppenaktivitäten die Anfangsstadien der Paarbildung beeinflussen könnten.

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