

COMMUNICATION AND SPATIAL RELATIONSHIPS IN A COLONY OF COMMON GRACKLES

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Abstract. Most communication among common grackles *Quiscalus quiscula* occurs at distances of less than a few metres in the noisy environment of a breeding colony. This report examines both the adaptations of communication to these conditions and the effects of communication in regulating individuals' spatial relationships. For each of six vocalizations and five action patterns studied in one colony, I consider variation in the form of the display, the circumstances associated with its use, and the responses it elicits. Each individual, male or female, has one characteristic, stereotyped song pattern that would facilitate individual recognition between mates. Variation in the components of vocalizations and action patterns is of two kinds: unidimensional, with either covarying or nested components, or multidimensional, with independently varying components, alternatives that have different implications for communication. The wide-spectrum sounds made by common grackles offer advantages in close-range communication in colonies, because the ease of locating such signals would minimize the cocktail-party effect, although they would have disadvantages in long-range communication. Most vocalizations of common grackles lack associations with specific responses or external contexts, a situation that should often characterize short-range communication between acquainted individuals. The responses to vocalizations vary with context, especially the initial spatial relationships and identities of the interactors.

Much of the communication between individuals in a society serves to regulate their spatial relationships (Tinbergen 1959; Marler 1968). Conversely, individuals' spatial relationships set limits on the possibilities for communication. The distance between communicators, in conjunction with properties of their environment, will determine the reliability with which they can detect each other's signals or discriminate differences between signals. The characteristics of communication, for populations in a particular environment, should therefore evolve adaptations to the typical spatial relationships of individuals. Among primates, for example, variable vocalizations are typical of close-range communication within groups, whereas stereotyped vocalizations occur more often in long-range interactions between groups (Marler 1965, 1973; Green 1975).

Communication between common grackles (*Quiscalus quiscula*, Icteridae), like many other colonial birds, primarily involves individuals no more than 1 or 2 m apart. This paper examines both the regulation of individuals' spatial relationships by communication and the effects of spatial relationships on the evolution of their forms of communication. The discussion suggests that adaptations for communication at short range in a noisy colony should appear in both the syntactics of communication, the

variability and structure of signals, and the pragmatics, the relationships of signals to the performer's states and the receiver's responses.

Ficken (1963), Snelling (1968), and Yang & Selander (1968) have previously presented basic descriptions of this species' displays. Present purposes require a systematic discussion of variation in displays, contexts, and responses.

Methods

On forty-one mornings between 5 March and 26 May 1971, I studied one colony of well-habituated common grackles in Bronx Park, New York City. Data pertain to four intensively studied pairs (B, G, D, JJ) and nearby individuals. Consequently, no information is available about possible variations in behaviour among different colonies. Many details of procedures are already included in previous reports (Wiley, 1976 a, b).

Vocalizations were tape-recorded with a Nagra III recorder and Sennheiser MKH804 directional microphone and later analysed on a Kay Sonagraph 7029A, with narrow- and wide-band filters (effective resolutions rated at 90 and 600 Hz for analysis range to 16 kHz), frequency sectioning, and amplitude display. Action patterns were studied in the field with particular attention to variation in form. My close attention to repeated performances of

each action allowed me to determine only the general nature of variation in each display.

To document the variation or stereotypy in temporal parameters of individuals' vocalizations, I measured intervals on sound spectrograms to the nearest 0.25 mm (0.001 s, somewhat less than the theoretical resolution of about 600 Hz⁻¹) and calculated the sample statistics with these values. Owing to the limited dynamic range of the spectrograph paper and variation in the machine's performance, measurements of the duration of a sound on a spectrogram can include significant imprecision. In measurements of the same vocalization on different spectrograms produced by the same machine, I occasionally found variations of 0.5 mm in my measurements. For certain brief calls, such as the chack and brtt calls described below, the standard deviations of my measurements were close to this error. For these calls, I have reported only the range of measurements. For measurements of other vocalizations, I give the mean and coefficient of variation ($CV = SD \times 100/\text{mean}$, where SD is the standard deviation). In measurements on individuals' songs, I have primarily used intervals between the onsets of different components of the song, rather than the durations of components, as the former measures should change less with changes in the relationship between the signal-intensity and the response-characteristics of the paper.

My information on the contexts and responses associated with each display comes both from timed samples of the behaviour of the four intensively studied pairs and from descriptions noted in the field. For certain displays, detailed notes of particular instances often proved more enlightening than my timed samples of interactions, which necessarily had to include only easily classified features of behaviour.

In this paper, I use the term 'display' to denote a class of similar communicatory motor co-ordinations, either vocalizations or action patterns, defined by a range of variation in the form of the co-ordination. These terms, referring to classes of co-ordinations, are distinguished from particular instances, termed 'performances.' The term 'signal' refers to those features of a performance available to a receiver.

Results

Vocalizations

Adult common grackles at their breeding colonies produce six structural categories of vocalizations, one of which is used primarily

by females and one exclusively by males. I witnessed no interactions with potential predators, a context for which this species, like other passerines, might have special calls. In addition, this study does not include calls used by nestlings or fledglings or by adults attending fledglings. Ficken (1963), without recourse to tape recording, also identified six vocalizations used by adult, breeding grackles. On the basis of his brief descriptions I can, with fair assurance, identify five of his six categories with four of my own. His terminology is included in parentheses below.

Chacks, chaas, and chitips, are all similarly noisy calls, which differ primarily in their temporal features (Fig. 1).

Chack (Chack). This sharp, harsh call, 0.02 to 0.04 s long, usually had indications of harmonics and reached maximum intensity between 2 and 4 kHz, although energy was spread over an even wider band of frequencies. To the ear, males seemed to have a slightly lower overall pitch for this call than did females. Each call was accompanied by a slight flick of the tail and wings and a slight extension of the neck. Spectrograms seem to reveal stable individual differences in this call (Fig. 1), although my sample of identified chacks is too small for definite conclusions.

Chacks varied in intensity depending on the circumstances. Males perched in the colony often chacked at intervals during periods when they were not singing or brtting (see below). At these times, when one male was chacking, others nearby were likely to be chacking also. Chacks in this situation were rather soft. Birds often began to chack if a person alarmed them by rapidly approaching the tree in which they were perched, and in this situation the chacks were usually louder.

Chacks frequently accompanied a bird's arrivals and departures from the colony, as did chaas and songs. Ordinarily, however, chacks were not associated with any particular external event. Birds perched in relaxed postures near their mates often chacked periodically, sometimes during interruptions in preening. Chacks in these circumstances appeared to maintain vocal contact between paired birds during periods of low arousal, although I noticed no temporal co-ordination between partners in their use of this vocalization.

Other than the tendency for chacks to become contagious among nearby birds, chacks often elicited no detectable response from other

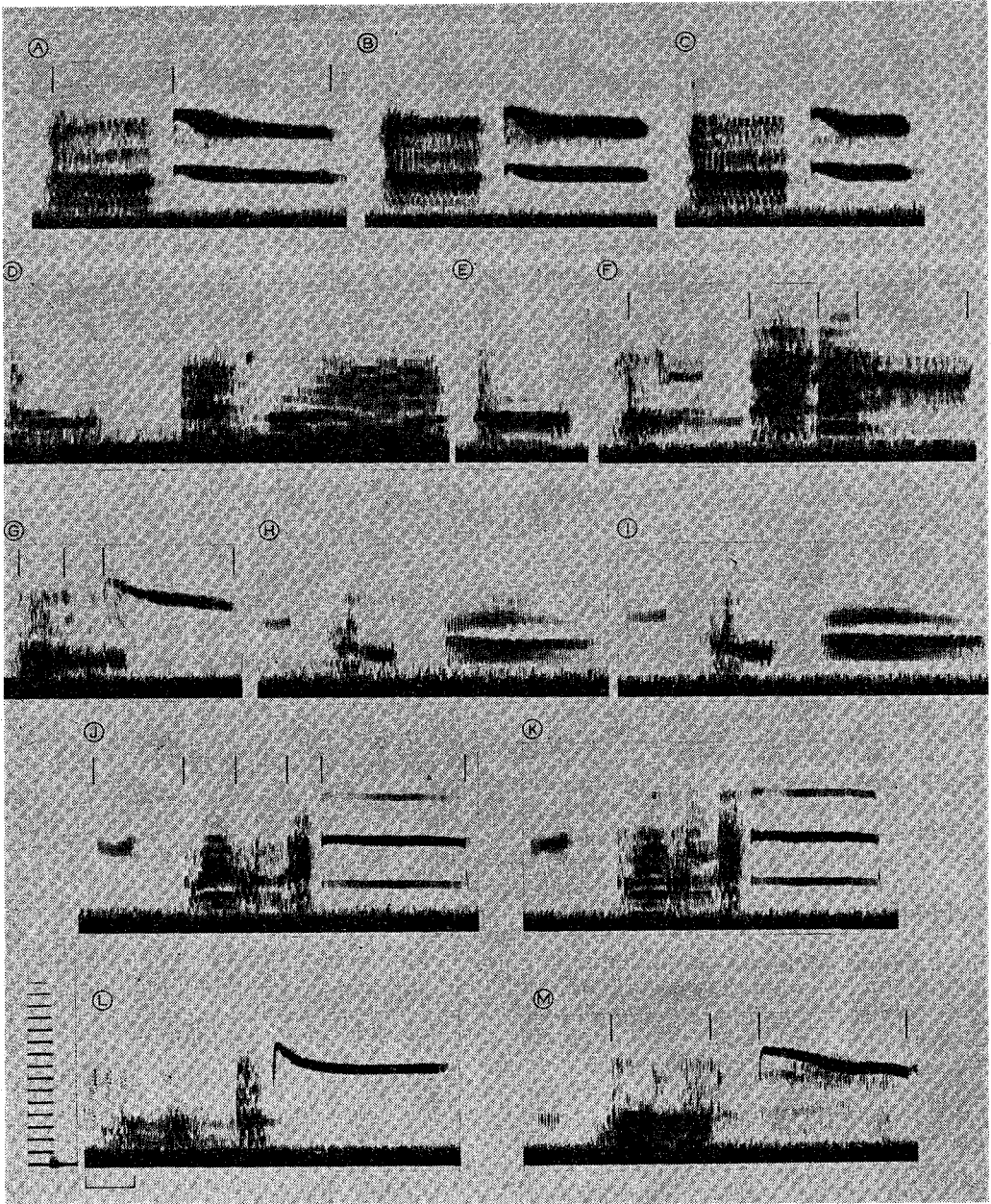


Fig. 1. Spectrograms of songs by individual common gracklers. A-C, male G on 19 March (A) and twice on 16 April (B and C). D, male D, full song. E, male D, abbreviated song. F, male B. G, male JJ. H and I, male V on 19 March (H) and 22 April (I). J and K, female G on 15 April (J) and 16 April (K). L, female D. M, female JJ. The vertical marks at the tops of certain spectrograms indicate the intervals analysed in Table I, in which the positions in each bird's song are numbered consecutively from the left. Frequency scale (lower left) indicates kilohertz; time scale is 0.1 s.

birds. When females vocalized on leaving the colony, their mates were more likely to follow (Wiley 1976b).

Chaa and Chitip (Waa). The chaa call, an extremely harsh, more prolonged call (0.15 to 0.40 s; mean 0.219; *CV*, 27.4; *N*, 21, including calls from several individuals) was used primarily by females. Although Ficken implies that this call is restricted to females, I definitely heard males use it, although rarely. Any one individual's chaa varied in intensity, duration, and number of repetitions. Chaa varied continuously from a single, brief, relatively soft variety to prolonged, repeated, intense ones. Two short, rapidly repeated chaa resemble a chitip, but chitips were themselves stereotyped enough to allow unequivocal identification.

It was my strong impression that each female had individually distinctive chaa. In the field, when two females uttered chaa within a short interval of time, I could hear that the timbre of their calls differed. In addition, on several occasions an identified male reacted to his mate's chaa before he could see her. Spectrograms suggest the existence of stable individual differences in the spectral properties of chaa (Fig. 1); however, a definite decision would require more identified tape recordings than I now have.

Females frequently gave chaa when approaching or approached by another grackle or simply near other grackles, during fights and chases, during flights between trees within the colony, whether near another grackle or not, during arrival and departure from the colony, and during group flights. Short, relatively soft chaa sometimes had no detectable relation to external events. The longest, most intense chaa accompanied supplantings, chases, and fights. Either the chased or the chaser or both would produce chaa, usually repeatedly. This vocalization therefore was often associated with taking flight or with decreasing separation between the subject and another grackle. It was most intense when these two situations coincided.

Chaa directed toward another female were likely to stimulate chaa in return. The response might also include avoidance or, occasionally, reciprocated attack. In another context, when a female gave chaa on taking flight from the colony, her mate was likely to follow; sometimes he vocalized in return (Wiley 1976b).

The chitip call, a variant of the chaa, consisted of two, rapidly repeated, harsh notes, 0.10 to 0.125 s apart. It was only heard from

females. The external situations and responses associated with this call resembled those associated with chaa. An additional indication that chaa and chitips have similar motivational and communicative properties came from differences in the frequency with which individual females used the two calls. Some females, including one observed repeatedly for 6 weeks (female 0), used chitips exclusively and never chaa. Other females, studied as intensively (D, G, B), never used chitips. Certain females, including JJ, definitely had both calls, although at least for JJ chaa were more frequent. All of these females used the two calls in similar situations.

Females on taking flight would occasionally introduce a series of chitips with a single chack-like unit: che-chitip-chitip.

Brrt (?Snarl). This distinctive call, exclusive to males, had an abrupt onset and termination (duration 0.06 to 0.08 s) and maximum intensity near 3 kHz (Fig. 1). It had a distinctive nasal quality that lacked extreme harshness. The strong side-bands in both narrow-band and wide-band spectrographic analyses indicate rapid (> 200 Hz) frequency or amplitude modulation (Marler 1969b; Watkins 1967). Spectrograms suggest the possibility of stable individual differences in this call, particularly in the pattern of side-band frequencies (Fig. 1).

Males often went for long periods without using this call. When they did use it, they often repeated it at intervals while perched quietly in the colony, although they would on occasion use this call instead of chacks when slightly alarmed by my approach. Later in the season, brrts usually had no association with particular external events. For instance, a male often gave brrts perched in relaxed posture near his mate's nest while she was absent from the colony. On the other hand, early in the season, males produced brrts in a great variety of situations. Males engaged in singing groups or group flights, near females or not, might use brrts repeatedly. Like chacks, brrts were often contagious among nearby relaxed males.

See (Peep). This prolonged (0.25 to 0.35 s) high-pitched (about 7 kHz), clear whistle (Fig. 1) accompanied both male and female precopulatory displays. Males alternated songs and sees during the head-down display (see below), while repeated sees accompanied the female's wing-quivering display (see below). The duration of this call varied considerably.

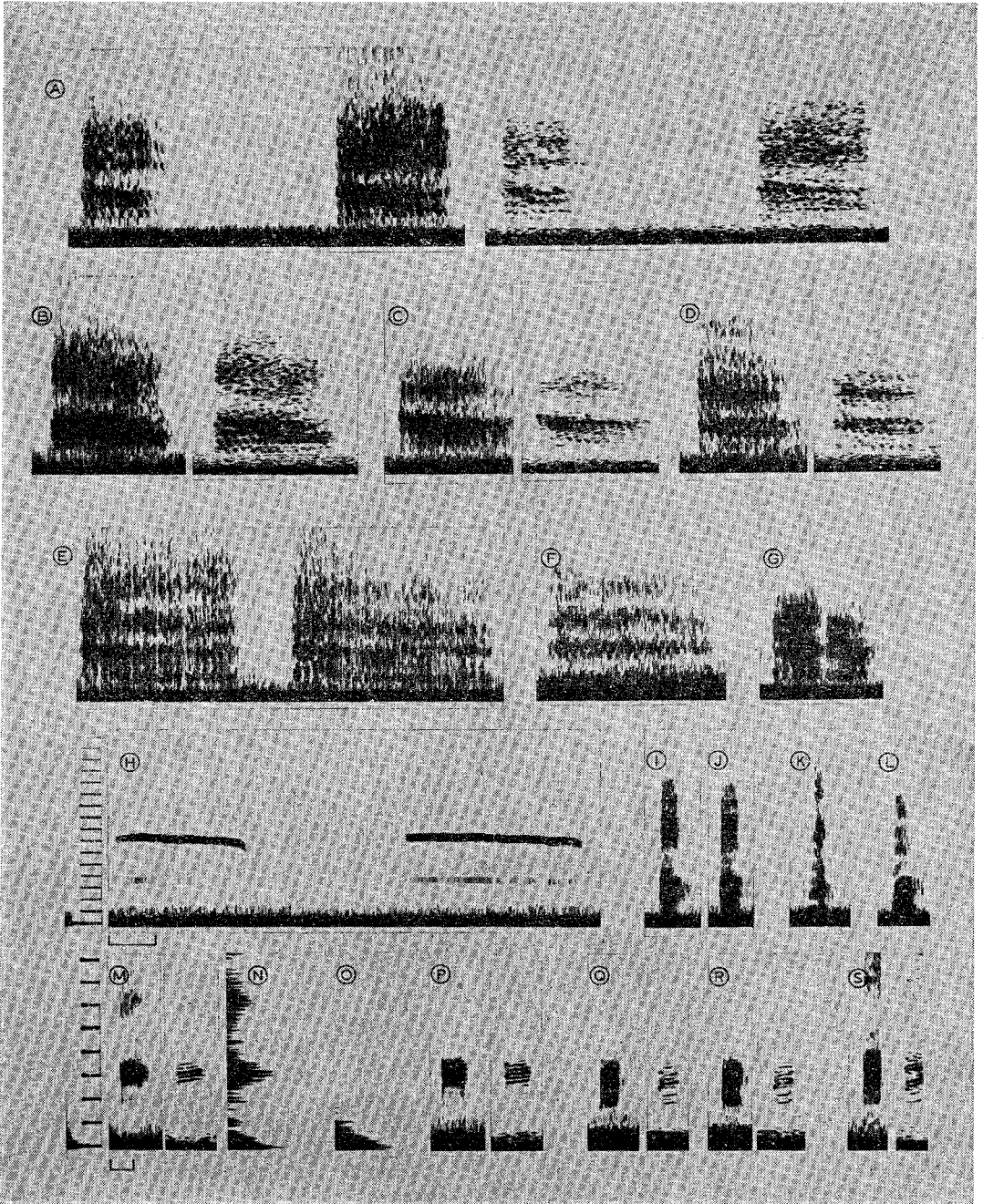


Fig. 2. Spectrograms of vocalizations by common grackles. *Chaa*: A and D, *chaas* by female D analysed with broad-band (left) and narrow-band (right) filters; B and C, two *chaas* by female JJ; E, two *chaas* by female G; F, female B. *Chitip*: G, unidentified female. *See*: H, unidentified female during wing-quivering. *Chack*: I and J, two *chacks* by one unidentified individual; K and L, two *chacks* by second and third unidentified individuals. *Brrt*: M, *brrt* by unidentified male analysed with broad-band (left) and narrow-band (right) filters; N, frequency section of preceding *brrt*; O, frequency section after the preceding vocalization to determine background noise; P, another *brrt* by the same individual; Q and R, two *brrts* by a second unidentified individual; S, *brrt* by male G. Frequency scales indicate kilohertz; time scales are 0.1 s. Note that M to S have larger frequency scales and smaller time scales than A to L.

Song (Squeak; Chuga). Each individual grackle had its own distinctive song. The differences among the males' songs were usually more striking and more easily learned in the field, but spectrographic analyses confirmed my conclusion in the field that females also had stereotyped songs with reliable individual differences (Fig. 2; Table I).

The songs of different individuals differed to the extent that the only species-typical features of the song were a duration between 0.2 and 0.8 s and the inclusion of a harsh segment with energy spread between 2 and 4 kHz. A high-pitched, relatively clear whistle, the referent for Ficken's term 'squeak', was absent from several males' songs, although it appeared in every song definitely identified as a female's. My observations therefore did not conform to Ficken's conclusion that females lack the high frequency components in their songs ('chugas').

The pairs that I followed intensively, several of them from before the formation of a stable bond, all maintained their individualized songs throughout. There were no indications that an individual ever changed the structure of its song

during the breeding season or, with the exception of abbreviated songs (see below), ever sang a second type. That an individual used the same song throughout the breeding season was confirmed for one marked male (V). This bird, trapped on 16 March and marked with blue paint on his tail and coloured bands, reappeared 2 days later and sang a distinctive song that I had first learned on 10 March. He did not nest in the grove of pines that I studied but visited them regularly. Although on several days he consorted with females, usually a different one each day, he never seemed to establish a pair-bond with any of them. He was last seen in the grove on 10 May. Throughout these 2 months he sang the same song type. Sound spectrograms of songs recorded on 19 March and, 15, 16 and 22 April, show only minor differences (Fig. 2). At least during any one breeding season, an individual grackle appeared to sing one stereotyped song.

The stereotypy of an individual's song extended to details of acoustic structure, including those parts of the song with wide spectra (Fig. 2). Variation was greater in the durations of the high-pitched whistles that terminated some individuals' songs (Table I). Frequency changes within this whistle and the presence or absence of harmonics remained virtually the same from one performance to the next, although the prolongation of the whistle varied. Another sort of variation, only heard in male B's songs, consisted of doubling the initial syllable in the song; this addition of one syllable at the beginning of the song did not change the timing or structure of the remainder. Patterns of stereotypy and variability were similar in males' and females' songs (Table I).

The situations in which grackles sang indicated that an important consequence of song was to establish the singer's identity. Early in the breeding season grackles sang frequently when a group gathered in a bare tree and during group flights. Grackles would often sing several times when another grackle, its mate or not, landed nearby or flew past. A mated grackle, either male or female, before incubation began, often sang unusually loudly when alone near its nest site. Usually the only overt reaction to a bird's song consisted of another bird singing in return. This response was especially prominent between paired birds (Wiley 1976b).

For a receiver within view of a singing bird, two continuously varying parameters might modulate the response to this stereotyped

Table I. Stereotypy in Temporal Parameters of Males' and Females' Songs

Individual (No. of days in sample)	Interval measured*	Mean duration (s)	Coefficient of variation	N
Male G (3)	1-2	0.230	1.3	18
	1-3†	0.490	10.7	18
Male JJ (1)	1-2	0.087	1.0	18
	1-3	0.164	0.8	16
	1-4†	0.426	3.8	16
Male B (2)	1-2	0.233	1.3	12
	1-3	0.365	1.0	12
	1-4	0.440	0.8	10
	1-5†	0.677	2.3	11
Female G (2)	1-5	0.437	1.5	13
	1-6†	0.691	3.3	13
	2-3	0.100	1.4	12
	2-4	0.196	1.3	12
	2-5	0.261	1.4	12
Female JJ (1)	1-2	0.191	0.8	13
	1-3	0.286	0.5	13
	1-4†	0.579	7.3	13

*Intervals between distinctive positions in each individual's song (see Fig. 1); the positions are numbered consecutively from the start of the song.

†Interval includes the duration of the final whistle, which is more variable than other components of the song.

acoustic signal. An individual's songs varied to some extent in intensity, a dimension that I could only estimate by ear. In addition, song was usually accompanied by a visual display, the song-spread (see below), and this accompaniment varied in a continuous manner.

Abbreviated song (?Snarl). Most males under intensive study occasionally produced a brief, harsh vocalization that sounded like the initial segments of normal songs (Fig. 2). Certain males (Y and AA) evidently only sang such abbreviated songs, whereas at least one male (B) under intensive study never did. Most males (G, D, O, JJ) used both complete songs and abbreviated songs, the latter more often after their mates had begun incubation. Male D, however, was the only one of these that used the abbreviated song frequently. No identified female ever produced abbreviated songs.

Abbreviated songs sounded vaguely like chaos, but sound spectrograms revealed that they possess more complex acoustic structure. Male D's abbreviated songs closely resembled, in spite of some slight differences, the initial syllable of his full song (Fig. 2). Each individual's abbreviated songs appeared identical from one performance to another and included reliable individual differences in details of acoustic structure. The individualities of different males' abbreviated songs allowed reliable identification in the field after some practice.

For those males that employed both kinds of songs, abbreviated songs seemed more likely in situations of low arousal, particularly when the bird was perched alone. Usually only rudiments of the song-spread display accompanied abbreviated songs.

Action Patterns

Grackles perform six action patterns in social contexts, all of which Ficken (1963) describes. My comments will amplify his treatment of the variability, contexts, and responses for these displays.

Song-spread (Ruff-out). This action pattern included at least six components: (1) erection of the contour feathers, particularly on the breast and belly and to a lesser degree on the head and neck, until the tips were well separated; (2) spreading of the tail; (3) dorsal rotation of the humerus, often with some extension of the legs; (4) constriction of the pupil; (5) song. Often components (2) or (3) began slightly later than (1). All three reached their maximum just before or coinciding with the onset of the

vocalization, and then during or just after the song all three abruptly returned to normal. The first five components showed considerable variability around the norm; sometimes a bird sang with no more than rudiments of the other five elements.

Song-spreads were in general less intense later in the breeding cycle, after the pair-bond was well established, and particularly when the pair had relaxed for a period or when one of the birds sang in the absence of its mate. This slackening in the intensity of display as the pair-bond strengthened could explain Ficken's (1963) conclusion that male song-spreads were more intense when directed toward another male. Early in the season, before affiliations between pairs had stabilized, males often displayed with full intensity to females, as well as to males. Female song-spreads rarely reached maximum intensity at any stage of the breeding cycle.

Grackles often sang in flight, either during a group flight or when taking flight with their mate. Males could perform a modified song-spread in these circumstances, as Ficken (1963) has illustrated, with some ruffling of the contour plumage.

Keeled flight. In this ostentatious form of flying, the tail was folded along its midline and spread into a deep V-shaped trough, often accompanied by somewhat exaggerated flapping. The wings beat rapidly through a wide arc and sometimes struck each other to produce an inconspicuous staccato sound. Keeled flight was rarely used by females. Males employed it particularly when approaching or leaving another male. Therefore it was especially frequent during arrival and departure from the groups of grackles that perched in the tops of trees near the colony early in the season and after bill-up displays near another male. Males accompanying their mates, especially early in the season, also often used keeled flight. Once a pair's affiliation was firmly established, though, the male tended to use keeled flight less often as he followed her.

Bill-up. This display consisted of an upward rotation of the head, so that the beak pointed nearly vertically. The movement varied from a quick toss of the head to a sustained posture with irregular upward jerks. It was particularly common early in the breeding cycle when groups of grackles gathered in the tops of bare trees near the pine groves.

Bill-up displays by males invariably occurred in response to another male's approach and usually resulted before long in one or the other

moving away. Males in these groups often perched no more than a metre apart without performing bill-ups, yet when a male landed close to another, one or both often began this display. Occasionally early in the season, an individual directed bill-ups toward a member of the opposite sex. I watched a female performing bill-ups toward an approaching male before she took flight followed by the male. Conversely, a male approaching a wing-quivering female once alternated between songs and brief bill-ups. Conflicts between tendencies to approach and avoid other individuals seemed particularly intense in these gatherings of unpaired birds early in the season.

In contrast, the paired birds under intensive study never directed bill-ups at each other. Once a male had paired, he rarely performed bill-up displays even toward other males. In my extensive timed samples of the behaviour of pairs after 31 March, I recorded only five such bouts of bill-up display.

Head-down. This complex display, performed only by males and directed toward females, involved (1) erection of the contour feathers, including those of the head; (2) elevation of the foreparts of the body; (3) spreading of the tail into a V-shaped cross-section; (4) dorsal rotation of the humerus and extension particularly of the carpal joint, so the wings from above formed a broad triangle; (5) downward flexion of the head, so the slightly opened beak pointed 60° or so below horizontal; (6) constriction of the pupil; and (7) alternating songs and sees. In this posture the male sidled along the branch toward the female, often within 10 cm of her. The male alternately twisted toward the female and then away, or back and forth in front of her, and slightly out of phase with these turning motions he would bow and rise. On the ground, the male in head-down display would circle around a receptive female until diagonally behind her, as Ficken (1963) has illustrated.

Each song alternated with one to several sees, although rarely the songs were omitted altogether. Coinciding with each song, the male often lifted his carpal joints slightly, a rudiment of the song-spread. Accompanying the sees, on the other hand, males occasionally quivered their wings slightly, a movement similar to the female's wing-quivering. The ruffling of the contour plumage during the head-down seemed closely similar to that in the song-spread display. The wing and tail movements, though, differed slightly in these two action patterns: the head-

down, more than the song-spread, involved extension of the carpal joints and keeling of the tail into a V-shaped cross-section. The angle of the beak during the head-down contrasted diametrically with that in the bill-up display.

Appreciable variation appeared in every component of this display. Particularly evident were differences in the extension of the wings. Although ordinarily not raised above horizontal, rarely the wings were lifted much higher. Often there were no rhythmical movements of the wings. Sometimes, however, the wings waved up and down at a rate of several times per second or quivered rapidly by flexion and extension of the carpus.

Males almost invariably performed the head-down display before and after copulation, but head-down displays actually culminated in copulation infrequently. These displays began to occur over a month before the first observed copulation, although during the initial phases of the breeding cycle males performed head-down displays at infrequent intervals. Once paired, they normally directed these displays only to their mates. During and just preceding egg-laying, when copulation began, head-down displays became much more frequent.

Of twenty-six bouts of head-down display directed at the male's mate, most were preceded by the male approaching the female (12) or the female approaching the male (7). The display also occurred immediately after the pair had landed together in the colony (4). Only four were preceded by female wing-quivering. There were indications that earlier in the breeding cycle, head-down displays usually followed an approach by the female, whereas later in the cycle nearly all head-down displays directed toward the mate followed an approach by the male. For pair G, three of the four head-down bouts early in the season followed the female's approaches, whereas all of the five bouts during the period of egg-laying followed the male's approaches ($P < 0.05$, one-tailed, Fisher Exact-Probability test; H_0 : no seasonal difference in sex of approaching individual). The rare head-down displays directed to females other than the male's mate (see Wiley 1976a) always followed the male's approach to the female.

Copulations followed nine of twenty-six bouts. Unless the female had begun to wing-quiver earlier, the male's head-down display usually did not evoke wing-quivering from his mate (8/22); when it did, copulation usually ensued (7/8). An unresponsive female would

repel a male approaching in head-down display by giving chaas, pecking at the male's head, or even lunging to peck at him. After several such responses males usually desisted. A male once ceased displaying after the female had simply given chaas. Females never took flight from a male in head-down display, whereas such close approach by a non-displaying male would cause immediate flight.

The importance of this display in promoting sustained close approach was especially clear during copulation. Head-down displays not only preceded almost all copulations but always followed copulation as well. During sequences of two or three repeated mountings, the male would maintain head-down display continuously except during the actual mountings. Such sequences would usually terminate when the female ceased wing-quivering and began to chaa and peck her mate, but on occasion the male terminated spontaneously.

Wing-quivering. This female display, with widespread similarities among passerines (Andrew 1961), involves (1) retraction of the head onto the shoulders, (2) upward rotation of the head so that the slightly opened beak pointed from 30° to more than 45° above horizontal, (3) elevation of the tail to about 45° above horizontal, (4) flexion of the legs, (5) partial extension and quivering (flexion/extension at the carpus) of the wings, and (6) repeated sees. As in other passerines (Hinde 1953), this display showed continuous gradation from rudimentary intention movements to full expression. In this continuous series, the wings reached full elevation before the tail, and the tail before the head. Occasionally a female would omit the rhythmic wing movements or the vocalization.

Although wing-quivering, like head-down, normally preceded copulation, this action pattern occurred at other times as well, when the female would not allow copulation. Weak wing-quivering first occurred early in the breeding season, although it was not frequent until around the time of egg-laying. Usually these early performances coincided with a male's landing near the female, but sometimes they followed the female's approach to a male. Often their interactions revealed no indication that the two birds were paired. Females in the groups of grackles that perched in bare trees near the colony early in the season would occasionally wing-quiver weakly. Also females

occasionally wing-quivered following a group flight, when several males alighted near her.

Females that had clearly formed pair-bonds still wing-quivered in contexts other than copulation. Females several times performed this display during or just after altercations with other pairs, usually when her mate approached her. Females carrying nesting material also occasionally wing-quivered weakly, and on several occasions females wing-quivered weakly in immediate response to hearing their mate's song at a distance. Of twenty-six bouts of wing-quivering recorded during my timed samples of paired birds, most occurred immediately after the pair had landed in the colony (7) or after one had approached the other (7). For nine of the bouts I could identify no particular preceding event.

These situations suggest that a wing-quivering female is in conflict between a tendency to remain near a male and a tendency to flee from him. Therefore, early in the season females used this display on occasions when a male landed nearby. As the pair-bond developed and mates began to associate closely, wing-quivering accompanied only situations in which her mate might attempt actual contact or following aggressive interactions with other pairs, when the female's tendency to remain near her mate would presumably increase. The delicate balance of antagonism and attraction between mates early in the season was revealed by one pair that sang together in a tree near the pine grove. The female weakly wing-quivered, then both performed several bill-ups, before both resumed singing.

Wing-quivering early in the season usually evoked no response from nearby birds. Occasionally several birds, including both sexes, approached the female. A female's mate also rarely responded except in those instances around egg-laying time. Of twenty-six bouts of wing-quivering initiated by paired females, six led to copulation, three evoked head-down displays from the mate but not copulation, and seventeen elicited no immediate response from the mate.

Copulation. Especially for the male, copulation varied considerably. The female would adopt extreme wing-quivering, with her beak nearly vertical and her cloaca everted, while the male, having moved close to the female's side in head-down display, fluttered onto her back. The male's beak usually pointed downward, and sometimes his beak touched his mate's. Wing movements,

after the male had settled, seemed primarily the result of shifting balance. The male on several occasions sang once after mounting. Copulations sometimes followed each other at short intervals.

Head-down displays and wing-quivering almost invariably preceded copulation, but particularly later in the season copulations often succeeded with brief preliminaries. The male's head-down display might include no more than two or three songs before he mounted, and rarely the head-down was omitted altogether.

Occasionally a copulation was interrupted by a nearby male that would immediately fly directly at the copulating pair. The intruder would retreat as soon as the pair separated. Otherwise, the male of the pair would supplant the intruder repeatedly. As a rule the pair resumed copulation within a few minutes after an interruption. On one occasion the female wing-quivered continuously until her mate had mounted once again.

Discussion

Variation Among Individuals

The need for a means of unambiguous recognition of individuals is especially marked in species, such as the common grackle, in which partners form affiliations before acquiring a nest site that can serve as a focus for their activities (Wiley, 1976a). Only the song showed consistent variation among individuals. My impressions in the field and limited spectrographic analyses, however, suggested that *chaa*, *chack* and *brtt* calls might also allow individual recognition.

The individuality of a grackle's song lay both in its temporal and spectral features. Most of the song, for some individuals all of it, consisted of wide-spectrum noise in precisely timed syllables. Yet the spectral quality of each syllable, although more difficult to measure, seemed as consistent from performance to performance as was its timing. The wide spectrum, however, would reduce the possibilities for differentiating signals solely on the basis of sequences or combinations of frequencies. The temporal patterns of intensity contributed a large measure of the diversity among individuals' songs. In certain colonial sea birds, individuals' vocalizations differ primarily in intensity patterns (Hutchison, Stevenson & Thorpe 1968; White & White 1970).

Variation in the Performances of Any One Individual

Almost all of the action patterns and vocalizations used by common grackles at their breeding colonies vary noticeably among performances by the same individual. Only the male's *brtt* call lacked clear variability. Each of these displays is a class of motor co-ordinations discretely separated by differences in structure from other such classes. Almost no performances, at least by adult birds, are intermediate between these classes. Within a class, though, the variation among performances by any one individual can be essentially continuous.

Patterns of variation in a display influence the information it can convey about the performer. The average amount of information in a performance of a display is the average reduction in a receiver's uncertainty about the sender's state, a quantity that will depend on the diversity of distinguishable variants of the display and the strength of their associations with different states of the sender. When concurrent components of a display vary independently in different performances, they can convey information separately about separate aspects of the performer's situation or internal state (Wiley 1975). The distinction between unidimensional and multidimensional variation in the parameters of a display therefore has important consequences for communication.

Variation is unidimensional if the performances of a display can be ordered in one dimension so that all parameters vary monotonically along that dimension. In the simplest kind of unidimensional variation, all parameters vary proportionately. In this case the level of any parameter can be predicted from the level of any other. Although such exact covariation in the components of an action pattern or vocalization probably seldom occurs, variation in the intensity of vocalizations like the song, and action patterns like the song-spread, seems to approximate such a condition. Variation with strongly covarying components has the effect of making the same configuration of stimuli either more or less salient to a recipient. Presumably the probability or intensity of response from the recipient would change accordingly.

The female's wing-quivering action exhibits unidimensional variation in the above sense, but with nested rather than covarying components. The components are ranked, such that any variant of the display that includes a component of high rank also includes all

components of lower rank, although the converse does not necessarily hold. In the case of wing-quivering, elevation of the head follows elevation of the tail, which in turn follows elevation of the wings. Action patterns with nested components could arise if each component were a distinct monotonic function of one variable of the animal's internal state. In a simple case, each component might have a different threshold of response to the same internal variable, for wing-quivering perhaps a tendency to allow exceptionally close approach by another bird. An action pattern with nested components presents a qualitatively different stimulus array at higher intensities, an arrangement that would presumably enhance a recipient's discrimination of intensity levels.

The variants of the male's head-down display do not allow ordering in a single dimension. Although I did not undertake a full analysis of this display, certain components, especially the wing movements, vary more or less independently of the others. In such a case, the variants of the display are not explained by one internal variable. Instead, different components would have to reflect weakly covarying internal variables or interactions among more than one variable. Such a complex action pattern might reveal through its particular array of components information about more than one variable of the performer's internal state and therefore might reveal conflicts in the performer's behavioural tendencies.

A display with multidimensional variation would incorporate little redundancy. Because the different components, insofar as they lacked correlation with each other, could convey information independently, the potential information content would be higher (Wiley 1975). On the other hand, because of channel noise, the probability of erroneous reception normally increases with distance, the low redundancy could reduce the reliability of communication in brief or long-range interactions (Wiley 1973). Among primates, complexly variable vocalizations are normally used in close-range interactions (Marler 1965, 1973; Green 1975), much as the head-down display of grackles.

Wide-spectrum Acoustic Signals in the Colonial Environment

Thorpe (1968) has drawn the analogy between the problems of communication in a dense colony and a problem of perceptual psychology,

the so-called cocktail-party effect (Cherry 1966). The problem is one of receiving a signal, which is coded inefficiently for contrast with noise, through a channel with a low signal/noise ratio. From the standpoint of a bird trying to identify its mate's call, the inefficient coding and low signal/noise ratio are unavoidable consequences of the colonial environment, as individuals' calls share similar spectral and temporal properties, and in any short period of time many different individuals' calls impinge on the receiver from approximately the same distance. Prior familiarity with the features of a particular signal would favour accurate reception (Howarth & Ellis 1961; Cherry 1966).

One property of a signal that can increase its contrast with simultaneous, similar signals is the ease with which the receiver can locate it. For instance, human subjects can more reliably separate a spoken message from random noise or separate two similar voices when the two sounds are received from different directions (Broadbent 1954). In a colonial environment, coding to increase ease of location should substantially increase the effective signal/noise ratio. Because a wide spectrum allows the receiver to make simultaneous binaural comparisons at many frequencies, the wide spectrum and abrupt changes of intensity in the song and other vocalizations of the common grackle and other colonial birds should maximize their ease of location (White & White 1970; Konishi 1973). Although the songs of some individuals contain nearly pure tones and harmonics, these tones are always preceded by broad-spectrum components with characteristic patterns of intensity, which would allow prompt localization and recognition. The only entirely tonal call, the see, is normally used when two birds are almost side by side in immediate visual as well as auditory contact.

Although a broad spectrum should facilitate locating the signal, this feature probably is not best for long-range transmission of a complex acoustic signal. Animals probably can achieve greater power per hertz bandwidth with tonal signals than with broad-spectrum sounds, an effect that would produce greater signal/noise ratios and extend the range of effective transmission. In addition, temporal patterns of intensity, important in differentiating broad-spectrum signals (see above), are obscured during long-range transmission of a sound. Scattering from non-stationary inhomogeneity

of the medium, including turbulence, would produce irregular fluctuations in the amplitude of a signal during transmission (Knudsen 1946; Rudnik 1947; Ingard 1953; Wiener & Keast 1959; Chernov 1960). Inhomogeneities, including dense objects and boundaries, would also add reverberations to the signal (Wood 1966). Although I can find no measurements of the spectra of amplitude fluctuations in atmospheric transmission of sound, the preceding references suggest that low frequencies (< 100 Hz) predominate (also D. Richards, unpublished observations).

To appreciate this constraint on the use of intensity patterns in long-range acoustic communication by animals, consider an acoustic signal that consists of higher frequencies modulated in amplitude at lower frequencies. The spectrum of an amplitude-modulated signal, described by its Fourier transform, consists of the carrier frequency and side-band frequencies separated from the carrier frequency by amounts determined by the modulation frequencies (Kinsler & Frey 1962; Wood 1966; Watkins 1967). The receiver's cochlea and central nervous system perform an approximate spectral analysis of the waveform received by the cochlea within a period determined by the time-constant of the auditory response and the difference limen for intensity (Gabor 1947; Gold & Pumphrey 1948; Békésy & von Rosenblith 1951; Littler 1965). The perception of amplitude modulation in an acoustic signal consequently varies with the frequency of modulation as well as the range of modulation (Stevens & Davis 1938). In particular, low modulation frequencies, in comparison to the reciprocal of the auditory analysis period, are perceived as changes in intensity, and high modulation frequencies as side bands.

When an acoustic signal is subject to low-frequency, irregular, amplitude fluctuations during transmission, these fluctuations will tend to mask low-frequency amplitude modulation in the signal and consequently obscure temporal patterns of intensity. Reverberations would further hinder the transmission of such patterns. Amplitude fluctuations might also impair discrimination of higher frequencies in a signal, because side-band spectra produced by any fluctuation frequencies greater than the reciprocal of the auditory analysis period would increase the difference limen for frequency. To compensate, the sender could encode information in frequency changes over a wide

range relative to the bandwidth of the fluctuations.

For long-range acoustic communication, animals often employ highly repetitive, and therefore redundant, intensity patterns; or relatively wide frequency changes in one or a few tones; or a combination of these two strategies. The long-range calls of certain forest primates, *Colobus guereza*, *Alouatta* species, and certain *Cercopithecus* species depend primarily on the first strategy (Marler 1968, 1969b, 1973). Many territorial passerines incorporate wide frequency changes of nearly pure tones in their advertising songs. The trills in the advertising songs of certain passerines, notably many Emberizinae, combine both features. For common grackles, among which almost all acoustic communication takes place at separations of less than a few metres, the advantage of broad-spectrum signals in facilitating location of the signal overrides any disadvantages in long-range transmission.

Specificity of Responses and Eliciting Circumstances

The criterion for the transmission of information between two animals is a response to the signal by the recipient or, more accurately, a contingent change in the response probabilities of the recipient (Marler 1961; Altmann 1965; Cherry 1966). As Smith (1965) and Schleidt (1973) point out, many behaviour patterns that seem clearly communicatory nevertheless rarely evoke specific, immediate responses from a recipient.

In part to circumvent this difficulty, Smith proposes to focus on the states of the performer associated with the production of different displays. By this means, he determines the information in an isolated signal, independent of context. He specifies in other words, the extent, to which he, as an errorless receiver, could reduce his uncertainty about the signaller's behavioural tendencies and identification as a result of receiving a signal isolated from its context, as for instance in the form of a tape recording or spectrogram. As Smith emphasizes (1965, 1968), the response of any socially appropriate recipient would depend not only on the information in an isolated signal but also on the signal's context in space and time. The receiver's perception of the signaller's situation and other actions, concurrent and previous, will affect the response.

Part of the complexity in communication among colonial animals such as common

grackles results from the simultaneous availability of signals in different modalities. Much of the communicatory effect of vocalizations such as the chack, chaa, and song of common grackles is probably to attract the attention of particular individuals. The ease of location and the individual specificity of the calls would permit this effect. Once the recipient's attention is directed toward the signaller, the recipient has available complex visual information in addition to the acoustic signals. The recipient's eventual response in such circumstances will depend on its reception of an array of stimuli in two modalities.

Most displays of common grackles also lack associations with specific external circumstances or internal states of the performer. Certain action patterns, especially wing-quivering, head-down, and bill-up displays, do occur in relatively specific circumstances, when the performer has particular tendencies to tolerate or resist unusually close proximity between two birds (see below). Other action patterns and all vocalizations lack associations with such limited contexts or internal states of the performer.

Communication at close range between acquainted individuals might not require that displays correlate with specific contexts or states of the signaller. For example, consider the calls used by female red-winged blackbirds (*Agelaius phoeniceus*) and common grackles when leaving their nests. Females of the former species have a conspicuous, specialized call for this occasion (female chatter; Orians & Christman 1968). Her mate is likely to spend much of his time at a considerable distance, perhaps 10 m or more, from her nest. A female common grackle uses chacks, chaas, or songs, vocalizations used in many other contexts, but her mate is likely to wait only a metre or two from the nest where he can easily see the female leave when she alerts him. In close-range communication between acquainted individuals, although the receiver's responses must often adjust to both the context and the internal state of the signaller, much information about context is directly available to communicators. The signals themselves would therefore not need to include this information; effective communication would not require associations of displays with particular contexts. Furthermore, in different contexts a display could be associated with different internal states of the signaller, without ambiguity for the receiver. Therefore when information about the signaller's context is

directly available to the receiver, the joint association of context, signaller's state, and receiver's response could remain high even with low first-order associations of displays with particular contexts, states of the signaller, or responses.

Communication and the Adjustment of Spatial Relationships

The external circumstances associated with the performance of certain displays often involve changes in the performer's spatial relationships with conspecific individuals. Many of the situations associated with chaa or chitip calls involve a deviation from the typical distance between two birds: either another individual approaches closer than usual, or the signaller moves away from its mate or its nest site, with which the mate is habitually associated. Chaa calls therefore often accompany the start or termination of locomotion, much like Smith's (1968) category of locomotory hesitance vocalizations. Because the chaa call occurs when another individual moves with respect to the stationary signaller and does not usually occur during locomotion without social significance, such as during solitary foraging, I suspect that the change in spatial relationships between individuals is more critical in the elicitation of this vocalization than is the change in locomotor tendencies.

Wing-quivering and head-down displays, respectively by females and males, are even more closely associated with special spatial relationships between the interactors. Wing-quivering evidently occurs when a female tends to allow closer than usual approach by a male. The distance involved changes during the season. Therefore, early in the season, females use this display when suddenly approached by a male, or sometimes when the female approaches a male, perhaps unknown to the female, at a distance as great as 1 or 2 m. Later, the female normally performs wing-quivering only when ready to accept copulation with her mate, when one or the other approaches unusually closely, or the pair lands together in the colony. Head-down displays were also associated with abrupt decreases in the partner's separation.

The bill-up display clearly occurs when two individuals, probably usually unknown to each other, find themselves close together. Even song sometimes seems evoked by the sudden approach of another grackle, even at as great a distance as 2 to 3 m. Often a male perched

quietly near his nest site will sing immediately after another lands in the same or an adjacent tree. In this situation perhaps the first requirement is to exchange signals for individual identification.

Among the responses to displays of common grackles, changes in spatial relationships again occur frequently. Another important class of responses, however, consists of contagious reactions, the repetition by the recipient of a signal similar to the one received. For most displays, the context and identities of the signaller and recipient influence the nature of the response. In Table II, I have summarized typical responses to five vocalizations of common grackles, according to broad classes of contexts.

Tinbergen (1959) first attempted to associate displays systematically with changes in the spatial relationships of interactors, and Marler (1968) has extended this procedure to primates.

Table II. Responses to Vocalizations According to Context

Vocalization	Context*	Usual responses
Chack	Close-range; between mates	Vocalization
	Long range; between mates	Approach, following vocalization
	Long-range; between ♂♂	Contagious reaction
Chaa/Chitip	Close-range; between mates	Distance increase
	Close-range; unmated birds	Distance increase, attack, fleeing
	Long-range; between mates	Approach, following, vocalization
Song	Long-range; unmated birds	Approach (rarely; see text)
	Close-range; between mates†	Vocalization; Song- answering
	Close-range; unmated birds†	Distance increase
Brrt	Long-range; between mates	Approach, following, vocalization
	Long-range; unmated birds	Vocalization (occasion- ally)
	Long-range; between ♂♂	Contagious reaction
See	Between mates	None identified
	Unmated birds	Approach Approach (rarely; see text)

*Close-range, less than about 1 to 2 m separation; long-range, greater than 1 to 2 m separation between interactors.

†Change between close- and long-range occurs at a greater separation for unmated than for mated birds.

Fewer than half of the displays of common grackles fall unequivocally into Tinbergen's and Marler's categories of distance-increasing, distance-decreasing, or separation-maintaining in their effects. Only see vocalizations, wing-quivering, and head-down invariably tend to decrease the separation between interactors; bill-up always tends to increase separation.

For other actions and vocalizations, the effects on the interactors' spatial relationships depend on the context, particularly the initial separation of the interactors and their possible affiliations. In Table II, note that for chaa calls, the response tends to differ depending on the initial separation of the interactors. Most calls evoke noticeably different responses from the mate than from other individuals. Only a few displays, like brrt calls, have no discernible effect on spatial relationships.

In close-range communication among common grackles, the spatial relationships of the interactors therefore often influence both the displays performed and the responses to displays. In general, it seems likely that the adjustment of spatial relationships among individuals or categories of individuals is a prime effect of many signals transmitted among the members of a society.

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