

COURTSHIP AND AGONISTIC BEHAVIOR OF THE COMMON GRACKLE, *QUISCALUS QUISCULA*

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THIS paper describes the courtship and agonistic behavior of the Common Grackle. The probable derivation, biological significance, and, in some cases, motivation and function of displays are discussed. Basic information on life history is available in Petersen and Young (1950) and Bent (1958).

The Common Grackle has a complex display repertory. This, when fully understood, will greatly contribute to our knowledge of social behavior in general. These observations can also be compared with similar studies of other icterids, thus furthering our understanding of evolution in this group.

This study was conducted from August 1957 to May 1960. Most observations were made at two colonies of about 15 and 20 pairs, at Ithaca, New York. In addition, birds were observed in captivity.

The Common Grackles of the Ithaca area are intergrades between *Quiscalus quiscula versicolor* and *Q. q. quiscula* (see Huntington, 1957).

DEFINITIONS

Display.—As used herein, refers to “. . . those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers . . .” (Moynihan, 1955).

Ritualization.—This is the process of display evolution.

Intention Movement.—This term includes various incomplete and low-intensity movements, which, as explained by Heinroth, reveal to the observer what the animal is “intending to do” (Marler, 1956).

Tendency.—Is used in the sense of Hinde (1955–1956) as given by Marler (1956): “. . . the readiness to show a particular type of behaviour as observed under natural conditions.”

Intensity.—Here means the degree of exaggeration in form of a movement.

Agonistic.—Refers to behavior concerned with escape and attack.

UNRITUALIZED AGONISTIC AND SEXUAL BEHAVIOR

Attack. In the Common Grackle this consists of biting, pecking, and scratching another bird. Intention movements for these activities and attendant locomotion are included in the definition.

A *peck* may be given with the bill either open or shut. Pecks seem weak and apparently never harm the recipient. In fact, some pecks involve no contact.

A *running attack* usually consists of holding the body in a horizontal position while running at the opponent. Gaping and/or wing- and tail-spreading may also occur.

Flying at another bird is a frequent form of attack. Flying at or running at usually result in the opponent leaving. A bird may *fly up* from the ground more or less vertically, extending its legs upward while orienting toward its opponent.

In *fighting*, the birds appear to bite and scratch each other repeatedly, and feathers are sometimes dislodged. When the birds are fighting in the air, they always fall downward rather than rising.

Escape. This is any avoidance movement stimulated by the object avoided.

Copulation. This refers to all cloacal contacts between male and female (see Figure 3). *Mounting*, a more inclusive term, refers to the male standing on the back of the female, whether or not copulation occurs.

During copulation the male's feet are placed on the female's upper back, and his tarsi are flexed strongly. The male's bill is pointed downward and his tail lowered to one side of hers, facilitating cloacal contact. At this point he flutters his wings rapidly, copulation taking but a second or so.

The female holds the bill pointed upward with head withdrawn between the shoulders. Her breast is lowered, tarsi flexed, and tail held upward and twisted to one side.

DISPLAYS OF THE COMMON GRACKLE AND THEIR PROBABLE DERIVATIONS

Displays are identified on the basis of their standardized and exaggerated form. Their communicatory function has been shown in several species, e.g., *Hylocichla* spp. (Dilger, 1956) and *Larus* spp. (Tinbergen, 1959).

Head Held Up.—This always involves pointing the bill up at any angle above the horizontal and is given only in the presence of another bird.

Other components occur in a wide variety of combinations. The bill may be either open or closed and may sometimes be tipped up and down slightly. The nictitans is often blinked arrhythmically, and the eyelids are sometimes partially drawn over the eye. The neck is held in any position from withdrawn to fully extended and the body anywhere from horizontal to nearly vertical. The breast plumage is usually sleeked but is sometimes relaxed or even fluffed while the head feathers are almost always sleeked, sometimes extremely so (see Morris, 1956, for feather posture terminology). The wings are usually folded, but their tips often droop below the level of the under tail coverts. The birds walk in various speeds and directions or remain stationary. Their orientation varies anywhere from directly toward to directly away from one another. Shifts

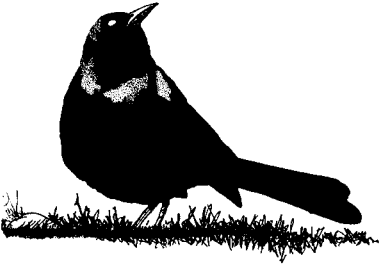
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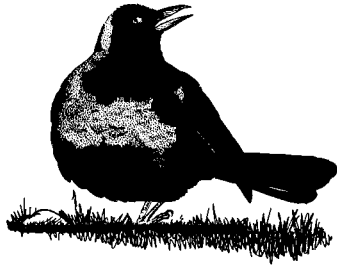
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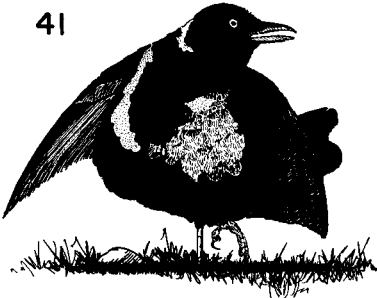
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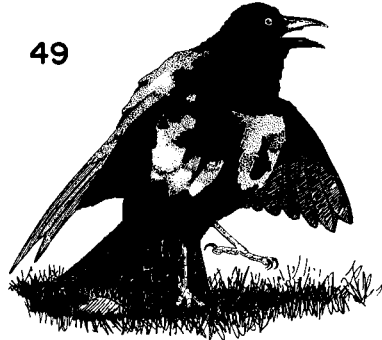
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in position of body parts, orientation, and speed and direction of movement may occur frequently and rapidly.

The *Head Held Up* is probably derived from an upward flight intention movement. Originally gaping was probably an intention movement to bite (see Marler, 1956).

The *Head Held Up* serves as a distance increasing display (see Tinbergen, 1959). Both nictitans blinking and eye closure hide the conspicuous yellow eye of the bird from the opponent. Since the eye is usually wide open in attack, these are probably "reverse movements" (see Marler, 1956).

Arhythmical Blinking.—This movement of the nictitans occasionally occurs by itself in agonistic encounters and is also frequently a component of other displays. The *Arhythmical Blinking* of the nictitans may be a ritualized form of rhythmic blinking. Rapid but rhythmic blinking was noted in several situations. During single one-minute observations of 12 hand-held birds, each blinked its nictitans from 3 to 63 times (\bar{x} 35.4). An incubating female gave 70 blinks in one minute when I approached her closely. Three caged birds aware of my presence gave 25, 60, and 68 blinks in one minute. Although the rate of nictitans blinking in undisturbed, lone birds was not measured accurately, they almost always blinked more slowly than those described above.

This movement, at least at higher rates, is associated with thwarted fleeing. In the Pied Flycatcher, *Muscicapa hypoleuca*, there was an increase in the rate of beating of the nictitating membrane when the bird "froze" in reaction to a hunting hawk (Curio, 1959).

Another possible derivation of *Arhythmical Blinking* is from the strong closure that occurs when the eye is touched or the bird "anticipates" its being touched, as when feeding young. Such protective closure might also occur during fighting.

Waa.—This vocalization of females occurs commonly in a variety of agonistic encounters.

Figure 1. Sequence from 16 mm motion picture film showing *Head Held Up* and *Ruff-out Squeak* displays in a male. Ten frames equal 0.33 seconds. Frame 1, male directing the *Head Held Up* toward a male behind him. Frames 11 and 21, beginning of ruffling and spreading components of the *Ruff-out Squeak*. Frames 31 and 41, male pivoting as the squeak component begins. Frame 49, the complete form of the *Ruff-out-Squeak*. The male has risen on his legs and is beginning to step forward. Frame 61, diminishing of the ruffling and spreading components as another *Head Held Up* begins. Frame 71, *Head Held Up* being given while bird is stationary. The opponent is to the right of the picture. Note the partial eye closure and nictitans blinking in frames 11, 21, 31, and 61. Also note the shifting of the iridescent highlights throughout.



TABLE 1

VARIATION IN INTENSITY, NICTITANS BLINKING, AND ORIENTATION OF THE MALE
RUFF-OUT SQUEAK DISPLAY IN THREE CONTEXTS

Context		Intensity		Blinking of nictitans		Orienting toward other	
		Low	High	Absent	Present	Absent	Present
Male alone	Number	18	0	13	2	Not applicable	
	Per cent	100	0	87	13		
With female not soliciting	Number	27	5	23	4	22	7
	Per cent	84	16	85	15	78	22
With male	Number	2	48	0	36	8	41
	Per cent	4	96	0	100	16	84

Snarl.—A male call similar to the *Waa* but typically higher pitched and clearer. It occurs in many situations: in hand-held birds, lone, undisturbed birds, during mobbing, in bouts of "song," but was never noted during intraspecific agonistic encounters.

Ruff-out Squeak.—This begins with a simultaneous spreading of the wings and tail and ruffling of the contour feathers (Figure 1). As spreading and ruffling reach their maximum, the bird rises up on its legs, utters the *Squeak*, flashes the nictitans arrhythmically, and may take a step or two forward. (The entire display lasts two to four seconds.) The *Squeak* component is the familiar "rusty gate" sound usually written as "*readle-eeek*," "*re-lick*," or "*scudle-eeek*." The sound of the *Squeak* seems consistent for each male.

The *Ruff-out Squeak* varies in several ways. A male once gave a *Ruff-out Squeak* with no apparent vocal component, and on several other occasions it was barely audible, sounding like "*screech*," "*eeek*," and "*peeku*."

Table 1 summarizes the form of *Ruff-out Squeaks* given toward females that were not *Soliciting* (see p. 59), toward other males, and by lone males. A comparison of the intensity (degree of ruffling and spreading), the presence or absence of nictitans blinking, and the orientation revealed some marked differences. Lone males always performed low-intensity ruffles and spreads and rarely flashed the nictitating membrane. Those given toward nonsoliciting females were roughly the same as those given by lone males except that they were sometimes of higher intensity, and the orientation component was occasionally present. Those performed toward other males almost always involved a greater ruffling and spreading, always included the nictitans blinking, and were usually oriented at the other bird.

The *Ruff-out Squeak* is often associated with other displays. It sometimes alternates with *Chacks*, occasionally with *Snarls*, and rarely with *Peeps*. One individual gave *Ruff-out Squeaks* followed immediately by *Snarls*. Once, another male performed the *Ruff-out* three times but instead of *Squeaking*, gave the *Snarl*. The *Head Held Up* often occurs before and/or after the *Ruff-out Squeak* (Figure 1).

Ruff-out Squeaks develop slowly in the young. Juveniles in early summer, when among other grackles at food piles, perform an activity that is probably an ontogenetic precursor of the *Ruff-out Squeak*. This incorporates ruffling of the contour feathers and a strong blinking of the nictitans but no vocal component.

The *Squeak* shows similarities to "song" of other passerines. An immature male gave gurgling noises (between *Ruff-out Squeaks*) that may be similar in form to the "warbling" during early "song" of the Song Sparrow, *Melospiza melodia* (Nice, 1943). Juveniles in winter also have short intervals between utterances, another characteristic of early "song" of the Song Sparrow (Nice, 1943). Another well-known characteristic of passerine "song" is that it occurs in lone birds as does the *Ruff-out Squeak*.

The *Ruff-out Squeak*, at least at close ranges, is probably a threat display since it frequently alternates with the more aggressive *Head Held Up* threat and during the last part of the nesting season may precede or even accompany attack.

The *Ruff-out Squeak* seems to have been derived from motor patterns characteristic of attack, combined with some patterns associated with thwarted fleeing, and a vocalization of undetermined history. The spreading of the wings and tail resembles the spreading sometimes accompanying a running attack. Rising up on the legs is probably derived from springing up to fly. Steps and pointing the bill toward the opponent are seemingly little ritualized components. Ruffling the contour feathers is more difficult to interpret, but is probably derived from the fluffing often seen if fleeing is thwarted in other situations.

Ruff-out Chuga. This display is typical of females. The visual component resembles that of the male *Ruff-out Squeak*, although it is typically less exaggerated. This display includes an unmusical vocalization sounding like *chuga* or, rarely, like *chuga-squeak*. One female gave *Ruff-out Chugas* followed immediately by *Waa*. Occasionally, females give *Ruff-out Squeaks*, but the female type was observed in only one male.

Chack.—This call is characteristic of the grackle in many situations, particularly during flocking, mobbing of predators, and in lone birds. It has several inflections.

Tail Flicking.—This is a preflight movement that occurs as a reaction



Figure 2. A "leader flight" showing three males behind the female. The lower four birds are viewed from below. Note the *V-tails* in the males and the aerial *Ruff-out Squeak* by the center male.

to various disturbances. It is an up-down movement (see Andrew, 1956).

V-tail.—This display is typical of males throughout the breeding season. The bird depresses its central tail feathers to form a V (Figure 2). The degree of depression varies from barely perceptible to deep. The *V-tail* is associated with flying, walking, and perching males, and on four occasions was noted in flying females.

Head Down.—This display always precedes copulation. In the highest intensity the bill is pointed downward and held in this position throughout, while the wings are lifted to the horizontal and extended slightly and the tail is spread, with some V-shape perceptible. The contour feathers are ruffled. From this position the display takes place in two phases, the first involving a *Squeak* vocalization and an orientation toward the female, and the second, bowing downward and then turning to one side accompanied by a *Peep* note, wing fluttering, and tail raising. The two phases are completed every two seconds in rhythmic alternation.

The higher intensities of the display have many variations. The *Squeak* phase sometimes differs from the above by: (1) increased ruffling of

the body plumage and spreading of the wings with each *Squeak*; (2) rising up on the legs with each *Squeak*; (3) *Squeaking* very weakly (on one occasion a male gave the *Chuga*). During the *Peep* phase the plumage is sometimes sleeked and the number of *Peeps* may vary from one to eight. Occasionally, a bird raises and extends its wings vertically and then flutters them. Nictitans blinking and eye closure may occur. Bowing between phases was only noted in birds that were displaying in places where the movements of their feet were restricted, e.g., on limbs or roof-peaks.

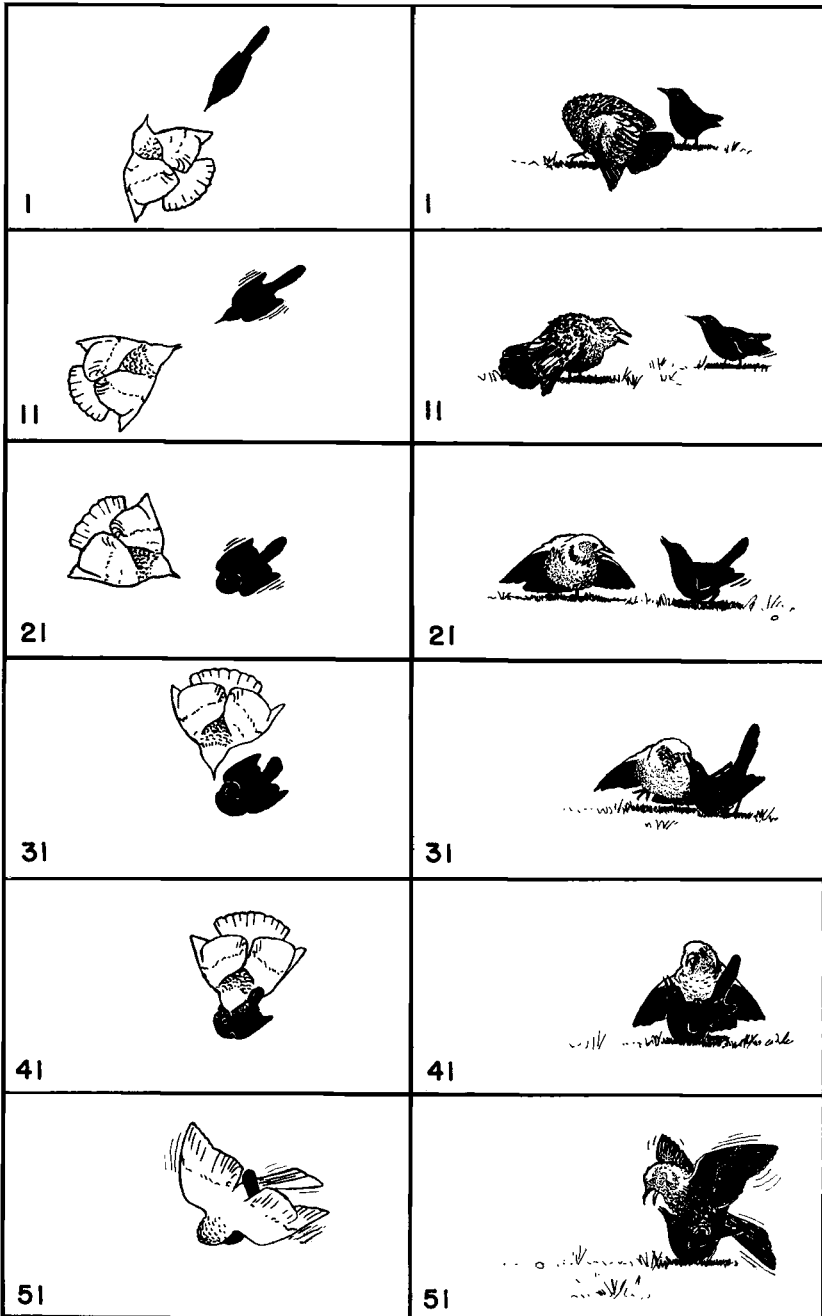
The *Head Down* has a "typical intensity" (Morris, 1957) in which the male holds his bill down and ruffles and spreads (Figure 3) while giving a rhythmically alternated series of *Squeaks* and *Peeps*. A frequent lower intensity of the *Head Down* only omits *Peeps*. At other times the male advances toward the female in a posture resembling the commonest *Head Down*, but without vocalization. An unusual, but simplest, *Head Down* consists of only pointing the bill downward. *Ruff-out Squeaks* may grade into a typical *Head Down* display.

Aerial *Ruff-out Squeaks*, although seen in lone males as well as those near females, are apparently linked with precopulatory display. These are almost always combined with a deep *V-tail*. Up to four may occur in rapid succession, sometimes alternating with *Snarls* or, rarely, a *Peep*.

The *Head Down* combines components of the *Solicit*, the *Ruff-out Squeak*, and the *V-tail*, with the addition of bill-lowering. Its derivation is obviously very complex. The pointing down of the bill is most probably derived from orienting toward the female during copulation. The occasional flapping of the raised and outstretched wings may also be derived from the act of copulation, i.e., the balancing movements of the mounted male, but on the other hand may be an intention movement of fleeing. The *Peep* phase of the *Head Down* is very probably derived from the *Solicit* and may contain the directly functional components of breast-lowering and tail-raising, as well as the more ritualized components of *Peeping* and wing-fluttering.

Solicit. This display resembles the position of the female during copulation. The *Solicit* may vary in several ways. Head-raising, wing-raising, and tail-raising may vary in degree, but are usually given together. *Peeping*, wing-fluttering, breast-lowering, and tarsal flexion are also often present in various degrees, and *Peeping* is sometimes uttered while in the "normal" resting posture.

As Marler (1956) has pointed out, the components of the female soliciting posture are mostly functional, aiding copulation by giving the male a place to stand, shifting the female's center of gravity, and exposing her cloaca. Wing-fluttering and *Peeping*, both ritualized components,



resemble the behavior of young begging for food.

A lone male gave a display on two occasions consisting of raising the tail to about 20 degrees, fluttering the wings, and uttering *Peep* notes. This display is similar to the female *Solicit*.

PAIR FORMATION

Pair formation of the Common Grackle begins in colonies as soon as the first females arrive. Two characteristic behavior patterns, flights and mutual displays, occur between each female and a group of males.

Pair-formation flights may be roughly divided into three types: leader flights, chases, and together flights. Each type may grade into the other. In leader flights (Figure 2), the males are usually in a compact group, occasionally straggling, behind the female, and the flight speed is moderate to slow. In chases, the males are behind the female, the flight speed is fast, and the female sometimes dodges. In together flights, the speed is also moderate to slow, and one or more males are above, below, at the side of, or even ahead of the female.

Pair-formation flights usually begin when a female flies from a tree with males following. Such flights are strong stimuli to males since they rarely remain when the female flies. Once in the air, males usually follow a female until she lands, although occasionally males land in one tree and the female in another. On a few occasions males flying by in another direction were "captured" by a nearby pair-formation flight and then followed along with the original males. Rarely a male took off from a tree first and a female followed and was followed in turn by another male or males.

These flights typically involve horizontal arcs and vary from about 15 to 500 meters or more in one direction. In this way the birds fly a long time and never leave the area of the future colony. However, rarely, flights take a straight course, and the birds go out of the colony area.

Figure 3. A sequence of precopulatory behavior, ending in copulation, drawn from 16 mm motion picture film. Ten frames equal 0.63 seconds. Numbers at lower left of each picture refer to frames. Frame 1, male performing *Head Down* display (including *Squeaks* and *Peeps*). Frame 11, male moving to the left but continuing to orient toward the female as she begins to flutter her wings. Frame 21, male in pre-mounting position with right eye closed. Female here beginning to adopt the *Solicit* by lifting tail and lowering breast. Frame 31, male approaching female more closely while still orienting to her head. She is now in the full *Solicit*. Frame 41, male mounting. Frame 51 shows copulation. The left column shows top views extrapolated from the side views on the right. Usually the female *Solicits* before the male begins the *Head Down* display (see text).



Flights may last 20 minutes or more but are usually less than a minute. They often take place at treetop level, but are sometimes higher.

Vocalizations given during pair-formation flights are also commonly heard in other contexts. Males often give *Ruff-out Squeaks* in flight, usually accompanied by a modified, slightly arhythmic wing beat or a glide. Rarely do they *Snarl*. The females frequently *Waa* in flight, often as a reaction to apparent thwarting situations, such as when leaving the tree, when a male glides toward her giving the *Ruff-out Squeak*, and when males catch up to her after takeoff. Females occasionally *Peep*, *Chack*, *Chuga*, and *Chuga Waa*. Many flights, however, are without vocalizations.

The *V-tail* is typical of pair-formation flights, occurring in exaggerated form during 37 per cent of 63 flights, and to some degree in an additional 31 per cent.

Females show an active interest in males. They occasionally follow males when they take off, but the males usually end following the female. Also, many flights have a male or males in front with the female following. On one occasion, a leader-type flight was interrupted when the two males engaged in a brief midair fight whereupon the female flew down toward them, and the flight was then resumed.

Males were seen fighting other males during flights on two other occasions and sometimes cut one another off. The proportion of males to females during 196 flights was 2 : 1 (129), 3 : 1 (47), 4 : 1 (17), 5 : 1 (1), and 6 : 1 (2).

Flights containing more than one female were seen on eight occasions, and most of these were together flights. During these flights the proportion of males to females was 5 : 2 (1), 4 : 2 (1), 3 : 2 (1), 3 : 3 (1), and 2 : 2 (4). In each case where landing was observed, the groups broke up into single females with a male or males.

Pair-formation flights are probably ritualized chases (leader flights almost certainly so) with fighting between the males reduced to a minimum, and fighting with the female now absent. Ritualized aspects are the frequent slow to moderate flight speeds, the *V-tail*, females following males, and the fact that males never catch the females, although they obviously could.

A pair-formation flight ends when the birds land. At this time, the birds engage in mutual display, which typically consists of males giving *Ruff-out Squeaks* and a female giving *Ruff-out Chugas*. The *Ruff-out Chuga* is the commonest female response, but they also give *Ruff-out Squeaks*, *Waas*, *Ruff-out Chuga Peeps*, and various forms of the *Solicit*.

Mutual display is not regular, but tends to occur in bursts with short

pauses. One male often *Ruff-out Squeaks* more often than do others, and different males may initiate bursts of this display.

During mutual display, males sometimes stimulate other males to leave by supplanting or fighting with them, or by advancing in the *Head Held Up*. Thus, there is active and apparently successful displaying and attacking in competition for females. In fact, males were never seen actually to fight in the absence of a female, although they often perform *Ruff-out Squeaks* and *Head Held Ups* at one another. Sometimes they also supplant and chase one another.

DEFENSE OF THE NEST-SITE AREA

Nest-site selection by the female begins after she is paired. During this period females walk about the colony area examining old nests. Males sometimes exhibit similar behavior. As soon as nest-site selection begins, the pair defends the site against other pairs.

Displays occurring during nest-site defense are essentially the same as those during pair formation; the *Head Held Up*, the *Ruff-out Squeak*, and the *Ruff-out Chuga* are often directed at other pairs. The *Waa* is the most frequent female call, and females sometimes *Waa* continuously for minutes.

Supplanting and fighting encounters were recorded during a two-week period from the beginning of nest-site selection to the completion of most nests. In 31 heterosexual encounters the male attacked the female in 27 cases and the female attacked the male in only 4. Thus, it seems that males are much more prone to attack females than vice versa. However, females attacked females (22) almost as often as males attacked males (29). In 43 of the male attacks, an attempt was made to observe the coincident behavior of nearby females. During 17 male attacks, the females were either not visible or sitting quietly. On the other hand, 26 of the male attacks took place when there was an interaction (displaying or attacking) between his female and another male or female. These observations indicate that males not only defend an area around the nest site but also their females against other males and females. Males defend their females away from the colony as well.

Observations of birds in or very near the colony compared with those of birds farther away reveal interesting differences. Often from two to four pairs silently approach the nesting area together. The females begin giving *Waas* when they are close, and typical nest-site defense behavior ensues among them when they land. Similarly, pairs that leave the nest-site area after being attacked are sometimes joined shortly thereafter by the same pair that had attacked them in the colony, but now perch peacefully nearby. On a few other occasions, one bird of a pair

attacked or displayed at one of another pair, and then both pairs silently left the colony together. When more than one pair forages near the colony, they often do not interact at all, or at most give *Ruff-out Squeaks* and *Head Held Ups*, unless a male displays at, or comes very close to, another's female. Only twice during the two-week sample period did a female attack another female more than three meters from the nest-site area. Thus, as in most birds, their location has important influence on their agonistic behavior. However, nest-site defense behavior may continue briefly outside the colony. Females that have been attacked may leave the area still giving *Waa* calls, and if birds have begun a fight in the nest site area, they sometimes continue down to the ground. Such fights are brief, however, and the birds then return to their nest sites.

Although agonistic behavior is quite pronounced in the nest-site area, the periods during which birds are attacking other birds are infrequent compared with the periods of relative quiet. Sometimes such quiet periods are broken by encounters involving up to four pairs producing a confusing sequence of flying about in front of the nest-site areas with some supplanting and much *Waaing* by the females.

Females sometimes display in unusual ways during nest-site encounters. Various forms of the *Solicit* often occur, apparently stimulated by nearby agonistic encounters. Females also give a complex of displays that normally occur singly, such as a *Ruff-out Chuga Waa Peep*, a *Ruff-out Chuga Waa Peep Waa*, and a *Solicit* with *Waaing* in place of *Peeping*. Similar complexes of displays occur in females leaving the nest during incubation (see below), and in females a short distance from displaying males at a food source.

INTERACTIONS OF THE PAIR

Interactions of the pair were studied during nest-site selection and nest-building. The basic pattern of behavior is again very similar to that shown during pair formation; i.e., the male usually follows the female when she flies to and from the nest site, and, when perched, they often engage in mutual display.

In typical paired flights, the female leads the male at moderate speeds. He often gives *Ruff-out Squeaks* and she often gives *Waas*. The male *V-tail* is very frequent when he is following his female (especially deeply in 73 per cent of 101 flights and to some extent in 19 per cent more), but was seen in the female only once in this context. Paired flights differ somewhat from pair-formation flights in that the former are typically shorter in duration, do not involve much "arcing," and are below tree-top level.

There were several uncommon variations of the typical pattern. These

included the female following the male, rapid wing-beating (moth flight) by the female, chasing by the male, and diving of the male at the female with *Ruff-out Squeaks*. Vocalizations occasionally heard were *Chugas* and *Peeps* uttered by the female and *Chacks* given by both birds.

Although males often perch in or near the nest-site area, they sometimes perch as far as 25 meters away. When females leave the colony, their mates usually follow. Males probably recognize their mates by visual clues such as physical appearance and location. On the return flight, females are usually followed by their mates.

Mutual display between the pair, the male typically performing a *Ruff-out Squeak* answered by a *Ruff-out Chuga* from the female, occurs throughout nest-site selection and nest-building. This sequence may be performed several times in succession. On three occasions, when a male foraged on the lawn and seemed hidden from the female's view, she answered his *Squeak* immediately with a *Ruff-out Chuga*. Since the *Squeaks* of males perched in and around the colony seemed to be distinctive for each individual, the female probably is able to recognize and respond to the *Squeak* of her mate.

Females rarely give other responses, such as the *Waa*, the *Ruff-out Squeak*, and *Peeps*, to the male's *Squeak*, and sometimes do not even respond. Mutual display is occasionally begun by the female.

Thus, each male usually keeps in close contact with his mate by perching near her, by following her, and by engaging in mutual display. Such behavior permits the male to be near his female when she solicits copulation, and to be frequently away from other males that often attack or threaten when he attempts copulation. It also enables him to defend her against the copulatory attempts of other males. The probable stimulation afforded by mutual display and following may also help to bring both sexes into synchronous reproductive condition, and following may also prevent polygamy.

SEXUAL BEHAVIOR

The precopulatory display of females (*Solicit*) and males (*Head Down*) has been described, as have mounting and copulation. Sequences involving the *Head Down* in and around the colonies were recorded in as much detail as possible every time they were observed. These observations were analyzed in terms of their location, form, temporal variation, function, and probable motivation.

The *Solicit* sometimes appears "spontaneously," i.e., in the absence of a male. It also differs from the male *Head Down* in that it is often stimulated by, rather than suppressed by, the agonistic displays of nearby males.

TABLE 2

FEMALE RESPONSES TO THE MALE *HEAD-DOWN* DISPLAY FROM NEST-SITE SELECTION (EARLY APRIL) TO EGG LAYING (LATE APRIL), EXPRESSED IN PERCENTAGES OF THE TOTAL (*N*) OBSERVATIONS FOR THREE PERIODS

<i>Date</i>	<i>N</i>	<i>Allows mounting</i>	<i>Attacks male</i>	<i>Flies or walks away</i>	<i>No overt responses</i>	<i>Some solicit</i>	<i>Ruff-out Chuga</i>	<i>Waa call</i>
April								
3-10	49	0	47	27	12	2	6	6
11-18	72	19	35	21	8	3	3	11
19-25	41	44	20	27	5	2	0	2

The *Head Down* occurs in many places, particularly in trees and on the ground and buildings in the vicinity of the colony, as well as occasionally in the nest-site area. This display is always directed at a female. It is rarely seen if a second male is near, in which case both males usually then give agonistic displays to one another.

Sequences were recorded from the beginning of the male *Head Down* toward the female until its termination. Such sequences were always discrete units, interrupted by a longer period of other activities. In a typical sequence ending in mounting, the female first *Solicits*; the male then walks rapidly toward her giving a *Head Down* of increasingly exaggerated form until he reaches her and mounts. However, more frequently males give the *Head Down* to females that are not *Soliciting*. Such sequences rarely end in mounting. A sequence, which is unusual because the female *Solicited* after the male displayed, is shown in Figure 3.

When the male gives the *Head Down* toward a female that is not *Soliciting*, the female typically attacks, walks or flies away, or gives no apparent response. Attacks by the female on the displaying male are always direct running or flying attacks, often ending in a peck at him. As many as 13 successive attacks by the female were seen. When the female flies or walks away from a displaying male, she usually does not vocalize or move rapidly, indicating more that she is "not interested," than that she is fleeing from the displaying male.

The first response of the displaying male to the attacks of the female is to fly off a short distance, turn away, or, most frequently, to continue to display. He is *never* seen to threaten or attack his mate before or after the *Head Down* despite her repeated attacks.

Sufficient sequences were observed during one spring to determine roughly the changes that took place as the breeding season progressed from nest-site selection until a few females were incubating (Table 2).

During this three-week period the most marked change occurred in the frequency of sequences that ended in mounting, from none in the first week to 44 per cent in the last. Attacks by the female, on the other hand, decreased during the same period.

The tendencies of the sexes during the sequences seem to be different. The male is always ready to mount if the female permits, but shows only a moderate tendency to escape from her, and no evidence of a tendency to attack her. The female, on the other hand, shows a strong but decreasing tendency to attack the male, little tendency to flee from him, and an increasing tendency to allow copulation. During the nonbreeding season the male is dominant over the female.

The fusion of motor patterns characteristic of at least four separate displays in the *Head Down* display suggests very strong selective pressures. Apparently it signals the sex of the male, since it is never given by females. It also indicates the male's readiness to copulate, since it always precedes copulation. It may signal lack of aggression because it incorporates the *Head Down* component (the "reverse movement" of the *Head Held Up* threat) and the female *Soliciting* call, and never causes the female to flee.

Since the *Head Down* rarely leads to *Soliciting* and subsequent mounting, its function may be primarily one of long-term, rather than short-term, stimulation of the female. However, the *Head Down* always precedes mounting and may stimulate the *Soliciting* female to maintain her posture until the male mounts. When the female is not *Soliciting* and the male gives the *Head Down* near her, it often stimulates her to attack. Since the female was never observed to attack her mate in any other situation, it seems that the *Head Down* component of his precopulatory display is the factor that leads to her attack.

The function of *Soliciting* is obvious. It stimulates the *Head Down* and mounting. When the female becomes receptive, she merely has to *Solicit* in sight of the male; the likelihood of copulation is then very great. The attacks of unreceptive females on displaying males, on the other hand, might function in the long-term stimulation of both members of the pair.

Both sexes have typical behavior patterns following mounting. The male often resumes the *Head Down* while the female often gives whirring movements of the wings that are seemingly identical with those normally occurring when the plumage is wet. Such wing-whirring occasionally follows *Soliciting* when the male does not mount. Occasionally, whirring of the wings does not follow mounting directly, but occurs after the female has first either attacked the male, flown away, or *Solicited* again. Males never whirl their wings except when they are wet, but occasionally

give two other comfort movements (bill-wiping and body-shaking) immediately after ceasing the *Head Down*.

BEHAVIOR OF THE FEMALE DURING INCUBATION

During the incubation period females give various displays upon leaving the nest. The female returning to the nest only gives the *Waa*, which is probably a reaction to passing near others' nest sites.

The frequency of vocal and visual displays in a sample (127) of 12 lone females leaving nests was as follows: Silent (10), *Waa* (51), *Chack* (12), *Peep* (2), and various combinations of *Waas*, *Chugas*, *Squeaks*, *Peeps*, fluffing, moth flight, glides, and *V-tail* (52).

The stimuli that probably act on the female while she incubates are the constant *Ruff-out Squeaking* of males and the vocalizations of other females leaving the nest. Apparently the tendencies aroused by these stimuli cannot be expressed because of the overriding tendency to incubate. As soon as the female leaves the nest, however, the other tendencies are manifested. An alternative explanation is that these are so-called "vacuum activities."

REACTIONS TO PREDATORS AND SUDDEN NOISE

When the colony was disturbed by sudden, loud noises, such as slamming doors, the birds often flew away together as a flock. Such flocking was not fortuitous, since the direction of flight of the flock differed in almost every case.

Mobbing was observed as a reaction toward a perched Cooper's Hawk, *Accipiter cooperii*, a flying Red-shouldered Hawk, *Buteo lineatus*, a perched Barn Owl, *Tyto alba*, a stuffed Great Horned Owl, *Bubo virginianus*, several flying Common Crows, *Corvus brachyrhynchos*, and man. Almost all of these predators induced flocking and abundant *Chack* calls, and occasionally *Tail Flicks*, *Snarls*, and *Waas*. The birds chased or dived at the crows and dived at the horned owl. My approach to the nest during construction induced flocking and *Chacking*, but after the young were fledged, strong *Tail Flicking* occurred also. Bent (1958) actually had his hat knocked off by a grackle when at the nest examining young. The Red-shouldered Hawk caused a large group to fly out of the colony together down into a pine tree where they perched silently and motionless for over a minute. They sometimes chased and dived at gray squirrels (*Sciurus carolinensis*), but never flocked in reaction to them.

Mobbing always involves attack and escape as well as flocking tendencies, which appear to vary seasonally and with the species, location, and activity of the predator.

The mobbing reactions are often extremely rapid and contagious, particularly flocking and *Chacking*. However, the means by which an entire colony becomes alerted and often manages to fly from the colony site up to the same tree within a few seconds are unknown.

DISCUSSION

The general pattern of reproductive behavior in the Common Grackle may be an adaptation to sociability and colonial nesting, which results in a great reduction in territory size. Thus, pair-formation flights and mutual display are probably adaptations in lieu of individual male territories into which females could enter and pair undisturbed by other males. The *Ruff-out Squeak* in which "song" is combined with visual display would be an advantage where close contact between birds is very frequent. Such displays occur also in other, closely related icterids that associate together during the breeding season, such as *Euphagus cyanocephalus* (Williams, 1952), *Cassidix mexicanus*, and *C. major* (Selander and Giller, 1961) but are apparently absent in *Euphagus carolinus* (personal observation), which nests singly. The *Head Held Up* threat, with its many variable components, presumably signals rather precisely the varying degrees of readiness to attack or escape. Such precision of expression would serve to reduce fighting, stress, and time wastage in a species where there is much close contact among individuals. The important role of the female in defending the nest-site area is an obvious result of the reduction of territory size. Since the female is not restricted to a territory, the male must follow and defend her against other males that may attempt copulation. By following his female, the male also greatly increases his chances of successful copulation without interference from other males. Mutual display between members of a pair and the long-distance recognition of the male's *Squeak* by his female may also be adaptations to colonial nesting. In addition, many of the above activities may serve to advertise the colony to new birds and probably help stimulate reproductive physiological readiness in the pairs.

Fighting in which feathers are dislodged occurs only in males that are in competition for females and in females in competition for nest sites, i.e., in those situations where the survival value of success would presumably be greatest. Such fights are apparently almost harmless to the combatants as they are in many species (cf. Lorenz, 1952; Dilger, 1960), which could easily kill or seriously injure one another.

There are several types of sexual dimorphism in the species. The *V-tail* is typical of males and is probably a long-range sex-recognition character. The distinct vocalizations of each sex accompanying the *Ruff-out*

are another form of sexual advertisement. The *Soliciting* is typical of females and the *Head Down* of males.

All of the displays of the male are given by the female (except *Head Down*), while the male gives all the displays of the female, even the *Ruff-out Chuga*. Thus, at least some individuals of either sex are capable of displaying in the manner of the other, but the threshold of these performances is apparently higher in the opposite sex. Such presumably sex-linked threshold differences (rather than absolute differences) are to be expected because of the ease with which they could be inherited, and are consistent with information available for other vertebrates. In addition, threshold differences in any behavior allow the species to retain the potential for rapid shifts of behavior in response to changing selective pressures, rather than losing such behavior patterns completely in response to their uselessness in any particular situation.

Threshold differences explain how the potential for the performance of certain behavior patterns may persist for a long time in the species. Although the evolution of displays should proceed in a manner similar to morphological features, displays differ from most morphological features in that under certain conditions they may never appear during the life of the organism. Thus certain displays can be rare in that they occur in all individuals, but only under unusual conditions, or rare in that they may be performed by some individuals and not by others. The actual extinction of all potential to give a display is probably extremely gradual. For instance Dilger (1960) has found in the genus *Agapornis* that occasional individuals will rarely perform displays that otherwise occur only in related species. This may be the rule rather than the exception. In the Common Grackle the *Ruff-out Chuga* and the *Ruff-out Squeak Snarl* were each characteristic of one individual male but involve merely the substitution of the typical female vocalization for the male *Squeak* in the former case, and the addition of a second call to the *Ruff-out Squeak* in the latter. Thus, although different from the typical displays of the male, these variants may be threshold differences.

The typical form of most of the visual displays of the grackle showed little variation among individuals, as would be expected from the need for accurate intraspecific signalling. The most variable call is the *Squeak*, which functions in intrapair recognition, and here variability would be an advantage.

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SUMMARY

Reproductive behavior patterns of the Common Grackle are described, and their probable derivation and biological significance discussed. Functional and causal analyses are presented for a few displays.

The most important displays are: (1) the *Head Held Up* threat; (2) the *Ruff-out Squeak* of the male, which is probably homologous to "song" but adds visual components, and the *Ruff-out Chuga*, the female counterpart; (3) the male *Head Down*, which is the precopulatory display combining four displays; and (4) the female *Solicit*, which invites copulation.

Pair formation consists of flights of two to six males and a female, and of mutual display (*Ruff-out Squeak* and *Ruff-out Chuga*) by these birds when perched.

Both males and females defend a small area around the nest site in the colony by threatening and attacking. Males also defend their females against other males.

In paired birds the male typically follows the female around, and when perched they may engage in mutual display. By staying near his female, the male is able to defend her against the copulatory attempts of the other males and to be often alone near her when she *Solicits* copulation.

Copulation is always preceded by the *Head Down* of the male and the *Solicit* of the female. During the period before egg-laying the male is always ready to mount if the female permits, but shows only a moderate tendency to escape from her, and no evidence of a tendency to attack her. The female, on the other hand, shows a strong but decreasing tendency to attack the male, little tendency to flee from him, and an increasing tendency to allow mounting.

Incubating females give displays when leaving the nest, which are probably aroused during incubation but are not able to be expressed until the females leave the nest.

Mobbing involves the interaction of escape, attack, and flocking tendencies.

Many reproductive behavior patterns of the grackle are probably adaptations to sociability and colonial nesting.

Serious injury during fighting was never observed in the wild. Fighting was confined to situations where the survival value of success is probably highest.

Behavioral differences between male and female are due mainly to threshold differences rather than absolute incapability. Threshold differences also help explain intraspecific variation. They are a convenient way of retaining potentiality for certain behaviors.

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