

## COWBIRD BEHAVIOR

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THE Cowbird (*Molothrus ater*) has been variously described in the literature as monogamous, polygamous, and promiscuous. As the species has been common in summer about my home in Nashville, Tennessee, I decided a few years ago to find out what I could about its territorial and mating behavior. I started color-banding in 1943, but did not undertake intensive watching until the following year. My observations were confined largely to the one and one-half acres about my home, especially to a small feeding place on the ground 25 feet from certain windows. In the breeding seasons of 1944, 1945 and 1946, I watched Cowbirds at various times of day from the arrival of the very first individual in March until the disappearance of the species in July. The birds came to the feeding place singly, in pairs, and in groups. Continuing my observations to some extent through the seasons of 1947 and 1948, I devoted several hundred hours, in all, to the study.

I attracted the Cowbirds with millet seed (the small, yellowish variety). In 1944 I confined feeding to a plot 21 by 5 feet near the house. At this gathering place, the scene of many intimidation, courtship and mating ceremonies, I gained a new understanding of the complex behavior of this highly social, parasitic species. That year my study centered in a population of 18 color-banded individuals (12 males and 6 females) and a few unmarked birds (three or more males and one or more females). In subsequent years, the population was not that large, but each year it included some birds returning from previous years. After 1944 I placed millet seed at other spots about the banding station so the activities of the birds were not concentrated at the main feeding plot.

My observations indicated monogamous mating, thus corroborating the conclusions of Herbert Friedmann, who studied unmarked Cowbirds at Ithaca, New York. He said (1929:171): “. . . if the birds are not really strictly monogamous, at least the tendency towards monogamy is very strong.” However, my findings in the behavior pattern differed rather widely from his. I observed several types of behavior not heretofore described, particularly *intimidation bows* and *guarding of mates*. I found no evidence of such true territorial behavior as that discussed by Friedmann, but there was much evidence that one pair gained *dominance* in a certain area. This area, the *domain*, may be all that is left of “territory,” and *guarding* all that is left of mate protection and isolation, in a social species whose breeding has become parasitical.

### SONGS AND CALL NOTES

Two songs are frequently used by male Cowbirds. Friedmann (pp. 166-168) described Song 1 as the “true song . . . , the *bub ko lum tsee*, as Wetmore writes it.” The *bub ko lum* part is a soft guttural gurgle, inaudible beyond 50 feet,

while the *tsee* is high, shrill, and sometimes considerably prolonged. Song 2, which Friedmann regarded as one of four call notes, he called the "flight whistle," describing it as a "thin, wheezy inhaling squeak, *whssss*, [followed by a] not so wheezy, exhaling whistle, *pseeee*."

Males at my banding station used Song 1 when posturing alone on a high perch, and when displaying before males in intimidation or before females in courtship. They used it less frequently in late summer than in spring and early summer. I have an early September record of a male singing and posturing alone in a tree.

Song 2 I heard more frequently than any other vocal sound of the species, although at times it was not complete. It was used as the male started to fly and as he alighted, but males sometimes flew without singing. Usually Song 2 seemed to serve as a means of keeping in touch with other Cowbirds. When feeding alone on the ground, a male often stopped, raised his head and sang, turned and sang again as if to send the note in a different direction, then stood still as if listening for an answer. Sometimes a male flew quickly toward the sound on hearing Song 2 in the distance. Song 2 was used by members of a feeding group. I knew of the arrival of a pair near the feeding station before seeing them because the male used Song 2 and the female "rattled" or chattered. This chatter note, a common utterance of the female, appeared to be her call to the male.

Notes that may have accompanied copulation I did not hear because of extraneous sounds. Friedmann (p. 167) described the male's mating note as "high, shrill, and in a descending scale." In 1944 and 1945 (four occasions) I heard the female use the rattle or chatter note just before copulation.

I heard short notes like *tic*, *phut*, or *kek* from the female as she fed alone, but never from the male feeding alone. The male used a note of this sort following a disturbance, however. Thus if the passing of a person caused him to fly up from the feeding place he would give a low-toned but emphatic *kek*. Sometimes he repeated this single note so rapidly that it sounded like the rattle of the female. On April 12, 1944, a pair used these notes and chatter as I walked past. I interpreted the notes as scolding or alarm notes. But on other occasions there was no response as I passed. On April 29, 1944, a male flew to a shrub and gave the short note as I removed a female from a banding trap. He waited some minutes until she was released from indoors, then followed her in flight, using Song 2. On another occasion, a different male used the short note as I removed a female from a trap.

#### POSTURING AND DISPLAY

The commonest intimidation gesture used by the male Cowbird is *bill-pointing*. Friedmann (p. 175) said of this display: "They have what might be thought of as an intimidation display which may be sufficient to drive off newcomers. This consists of pointing the bill towards the zenith when near another male."

After watching hundreds of displays, most of them on the ground, I decided that certain displays had not yet been described. Elaborate "toppling-forward" bows, with wings and tail spread and bill or head touching the ground, were made in intimidation or threat. The *peck-gesture* was another sort of threat. In this display, the plumage was usually puffed, the wings spread horizontally or raised vertically, and the head thrust forward. Sometimes there were a few running steps or a flight toward the other bird. At times the display ended in actual pecking or fighting. Both of these types of intimidation display were used toward other male Cowbirds and occasionally toward a Mourning Dove (*Zenaidura macroura*), Grackle (*Quiscalus quiscula*), Brown Thrasher (*Toxostoma rufum*), or House Sparrow (*Passer domesticus*).

I saw five fights between male Cowbirds in April, 1944. During that same period, I was witness also to a peck-fight between a male Cowbird and a Brown Thrasher. The Cowbird was the aggressor. In May, 1944, I saw a male Cowbird viciously attack a House Sparrow. In April, 1945, I saw a male Cowbird strike at a female Cowbird three times within a few minutes, once while flying and twice on the ground. The attack appeared to be hostile. Nice (1937:154) mentions five instances of fights in April between male Cowbirds at Columbus, Ohio. Friedmann (1929:175) knew "of no instance of two male Cowbirds fighting."

I saw female Cowbirds intimidating other Cowbirds of both sexes through *bill-pointing*, *peck-gestures*, and (very rarely) through bowing. On June 15, 1944 and April 9, 1945, I saw fights between females. Friedmann described no female display or fighting.

Another type of behavior, indulged in mostly by the dominant male of each season, was a repetition of trips to the water pan between displays. Sometimes after running to the pan, he merely dipped his bill. Sometimes he failed to drink. All this seemed to be substitute behavior in moments of excitement.

#### COURTSHIP

Bows extended in greeting or courtship by males to females were less elaborate than intimidation bows. Greeting bows of this sort varied considerably; sometimes they were only a nod, accompanied by ruffling of the neck plumage, sometimes a deep bow, involving spreading of wings and tail, sometimes a mere relaxing of the wings. Occasionally a male bowed in greeting just after stretching tall, or pranced beside the female before bowing. On April 19, 1944, when 5M was displaying to 2F, he seemed to rise as he braced himself with tail against the ground just before bowing. When displaying alone in a tree, he often terminated his bow with a bill-wiping gesture.

The dominant female of the season displayed by relaxing her wings, puffing her plumage, vibrating her tail, and quivering her wings. These displays were, I believe, connected with courtship and mating.

In pair formation ceremonies, both birds indulged in stretching, usually of a sidewise sort. This I witnessed on April 10, 1944, March 24, 1945, and March 30, 1946, the two participants being dominant.

On two occasions I saw a male toying with a dead leaf or a piece of debris while bowing to a female (April 8 and May 29, 1944).

A common type of behavior was *guarding*. In this maneuver, the male ran quickly between a female and one or more males, and attempted to remain between them while the group was feeding or otherwise engaged. While guarding, a male sometimes bowed low to another male, then turned to extend a shallow bow to the female. The dominant female occasionally guarded her mate from another female. Guarding was practiced mostly by the dominant pair of a group, but I occasionally saw a visiting male guarding the female accompanying him.

#### COURTSHIP AND CONTENTIONS FOR SOCIAL DOMINANCE

The first Cowbird of the 1944 season, 1M, arrived March 16. (He had been banded as an adult on June 7, 1940, and had returned in March, 1942 and April, 1943.) On March 23, 1944 another male arrived. I banded him and called him 3M. I saw these two males separately, several times, feeding peaceably with Mourning Doves, Cardinals (*Richmondia cardinalis*), Red-eyed Towhees (*Pipilo erythrophthalmus*), Slate-colored Juncos (*Junco hyemalis*), House Sparrows, and Field Sparrows (*Spizella pusilla*). The Cowbirds sometimes scratched in their desultory manner. Scratching was prefaced by a slight hop which ended with the feet spread apart, one beyond the other or in a side-wise spread, as if one foot had slid backward or to the side. I heard only the flight whistle those first few days, but on March 22, 1M, perching in a tree above the feeding place, postured and used Songs 1 and 2 for several minutes. I saw no other bird anywhere in the vicinity at the time.

On March 26, a female came with 1M. The following day, at the food, he ran to her with puffed plumage and bowed each time she stood still, but she always moved away. I caught and banded this female on March 28, naming her 1F. For several days 1M and 1F followed each other and fed together, the male continuing his displays. But early on April 1, I saw 1F feeding with an unbanded male that displayed to her. Suddenly 1M swooped down and attacked this male. After a brief fight, the unbanded male moved to another feeding spot a few feet away and 1M joined the female. Once she moved toward the unbanded male, but 1M ran between them, guarding her. That day I saw 1M and 1F feeding together several times.

On April 2, other Cowbirds arrived. Near noon, 1M, 3M, and two unbanded males were feeding amicably within six inches of each other when suddenly a Brown Thrasher appeared. 1M instantly assumed a fighting posture (peck-gesture) toward this bird and the thrasher returned the gesture. They hopped at each other several times as if striking bills. As the thrasher flew off, two Cow-

birds, apparently the banded ones, entangled in a fight, rolling on the ground. Then all four Cowbirds flew off.

On April 3, 1F came at 8:00 a.m. with an unbanded male which I trapped and named 4M. (This visitor did not appear again until June 14, on which date he stayed briefly.) On April 4, 1M and 1F were together. Once I saw him walk completely around her. Though her wings were relaxed in courtship display, she evaded him.

Early on April 6, two strangers appeared, a transient female and a male Cowbird that remained in the area. These I banded, naming them, respectively, 3F and 5M.

On April 8 two color-banded females arrived, 2F (banded in April, 1943) and 5F (banded in September, 1942, retrapped in March, 1943). That day nine Cowbirds visited the feeding area singly and in groups—1M, 3M, 5M, three unbanded males (one with an injured foot), 1F, 2F, and 5F. There were many encounters for supremacy among the males. Some of these encounters may have resulted directly from courtship displays before the females.

At 10:25 a.m. an unbanded male, landing near 1F, threatened another unbanded male by bill-pointing, causing the latter to cower and run. At 10:30 an unbanded male landed near a banded female Mourning Dove and raised his wings as if to fight. The dove retaliated in kind, so he retreated and fed five feet away. At 10:40, 3M, accompanied by two male and two female Cowbirds, arrived and 3M displayed to 2F. At 10:50, while 5M and a dove were the only birds at the feeding plot, 1M arrived and ate amicably beside 5M until an unbanded male arrived. 1M now raised his wings and ran at the newcomer with the peck-gesture, but the newcomer merely moved a bit and 1M soon joined him. They fed briefly and the two flew off, 1M leaving first. At 11:15 I saw 3M attempting to chase 5M and an unbanded male by running at them with the peck-gesture. This did not put them to flight. 3M repeated the hostile gesture to the unbanded male, but all remained to feed. Then 1M arrived. The three other males now flew, and 1M, alone, strutted a bit with up-pointed bill. As 2F and an unbanded singing male arrived, he amicably joined them, the female feeding close to him for a brief period. At 11:30 1M and 1F arrived together. Presently 5M landed nearby. 1M ignored 5M, but twice displayed to 1F, with puffed plumage, extended wings, and Song 1.

At noon a peculiar ceremony took place between 1M and two unbanded males. Although feeding some distance apart, each displayed by puffing his plumage and dragging his tail. After five minutes of this behavior, they formed a triangle a few inches apart, all facing inward. They repeatedly bowed, bending forward until their bills touched the ground, meanwhile spreading their wings and tail. After a minute-long performance, one walked away, while the other continued to display to 1M. 1M moved off but rejoined the displaying one. Both then bill-pointed several times as they walked. The unbanded one bowed low to 1M, who suddenly flew at him, chasing him some feet, then the three birds flew.

During the next three hours, once an unbanded male fed amicably with 3M, and once 3M and 2F fed together while an unbanded male ran around them, 3M bowing to him until the unbanded male went to the far end to eat alone. Later 1M fed amicably with an unbanded male, but when another unbanded male arrived, he ran at the second with a peck-gesture; then all fed amicably together. 1F and 2F appeared at the food several times, each accompanied by one or two unbanded males.

At 3:22 p.m. 1F arrived, alighting in a tree near the feeding place. On previous occasions she had rattled once on arrival, but now she reiterated her call. As if in response, an unbanded male alighted in a nearby tree. Facing her, he gave two bowing displays. When she flew off, he followed her. Presently she returned to feed. An unbanded male was still following her. On being joined by 3M, the unbanded male started a display to 1F. He made a quarter turn toward her, bowing slightly, continuing to follow her as she fed, circling about her as he puffed plumage and bowed. In the course of these displays, he pecked at and picked up a piece of debris. A few seconds of feeding followed the courtship display, whereupon the males faced each other in bowing ceremonies. Each time a male moved, 1F ran a bit, avoiding any close contact with either.

At 3:40, 1F and 1M arrived, joining the sole occupant of the feeding plot, an unbanded male. A low-flying male appeared but did not alight when 1M assumed a fighting posture. When 3M arrived somewhat later, he came near 1F, and 1M guarded her as they moved about feeding.

There was more bowing and gathering in groups for the rest of the day, with 3M attending 2F, intimidating 5M with very low bows, and simultaneously guarding the female. Once when 5M and an unbanded male met, the latter retreated at 5M's bowing. Shortly after 5:00 o'clock, when four males and a female were present, another ceremony occurred. After 5M had displayed to an unbanded male, 1M bill-pointed as he walked toward them. The unbanded male bowed low to 1M in response, backing as he did so. 3M, who had been feeding several feet away with 2F, joined the other males and the four birds formed a square, facing inward. They bowed repeatedly, touching the ground in elaborate intimidation display. 3M withdrew to join the female but soon rejoined the posturing males. Presently 5M walked off a short distance, leaving the others to bow for another minute. The five birds flew off in a group.

Early the following morning, April 9, I caught the two unbanded males, naming them 6M and 2M. 6M stayed only until that evening and was not seen again. 2M became the dominant male of the season, spending more time at our place than any other Cowbird. Between April 8 and July 1, I saw him 249 times. He apparently considered himself the proprietor of the feeding plot and environs. He became the mate of 1F, displacing 1M, who had courted her and threatened the other males. On April 9 I saw neither 2M nor 1F, but 1M and 6M came to feed, sometimes amicably.

On April 10, I did not see 1M. He made his final appearance April 11 when he came for a few minutes to feed with an unidentified male.

#### PAIR FORMATION, MATING, AND SOCIAL DOMINANCE OF THE PAIR

From April 10 on, 2M guarded 1F and intimidated other males. At 4:50 p.m. on April 10, I noted the following: "3M at food, 2M and 1F arrived together, 1F rattled twice, 2M pointed bill, ran to 3M, bowed to ground twice with Song 1, female rattled, 2M again bowed very low to 3M without song, ending by touching bill twice to ground. He returned to female. At 5:06, began another series of 4 low bows to 3M, followed by a shallow bow and plumage puff to female. 5:08, standing midway between 3M and the female, 2M bowed 4 times to 3M who flew; 5:10, 2M, now feeding near the female, ran, pecking the ground. For 8 minutes they stayed together. She had wings relaxed, slightly extended from sides. When the male fed close to her, she quivered the wings briefly. Both occasionally fluffed neck plumage. Male stretched once, female stretched twice during this period. This was a sidewise stretch—wings were raised slightly, then one leg was extended backward as the corresponding wing was spread groundward. Then he approached her with a quarter turn, head lowered in the manner of a domestic cock. They flew, but she returned. She stretched again with upraised wings, then bent legs at metatarsal joints. A Brown Thrasher arrived just then; 1F assumed the peck-gesture to the other bird."

At 7:45 that evening, the pair (2M and 1F) were feeding when an unbanded male arrived. Facing the male, 2M made six or seven elaborate bows, interspersed with two shallow bows as he faced the female, guarding her. During the next several days, I saw the pair together many times. Displays which I noted included "a dancing toward her, preceding the shallow bow" and "the quarter turn side bow (facing diagonally)."

#### COPULATION

When 2M came to the feeding place on the morning of April 16, he was alone. Alighting in a tree he used Song 1, flew to the ground to feed, sang several songs, indulged in some mild posturing, ran to the water pan, then ran back to the food. Six minutes later, he gave a shallow bow, ran again to the water pan, and flew off. At 10:18 he was back. He sang several songs on the ground, usually No. 2. At 10:23, 1F arrived with her rattle call, and alighted in a tree above him. He flew to her, alighted on a branch beside her, and bowed. She squatted, elevating her tail. He mounted briefly then hopped to a limb. She remained quietly for a few seconds before flying to the ground to feed. He followed, displaying there a few times.

Twice later that season I witnessed copulation between the pair. On April 20 at 9:00 a.m. both were in a tree above the feeding plot. He sang and she rattled just preceding the mating act, which was accompanied by considerable fluttering. The male followed her down to feed but soon flew off. Then an amus-

ing three-minute episode occurred. He returned immediately with another female, 5F, who had been here the previous two seasons. He and 5F stopped within a few feet of his mate. The latter approached 5F with up-pointed bill and bowed fairly low to her. The male came between them. 1F walked back to her feeding spot. The male joined her but only momentarily, for he was soon back with 5F. Again 1F walked to 5F, circling slowly around her, bill-pointing. 5F started to leave, but once more 2M walked between the females. This time 5F flew, 2M after her, 1F trailing. About three-quarters of an hour later, 1F came back, followed closely by 2M, who approached her with puffed plumage. She ran at him, striking him with her bill. He moved away, but she walked after him and followed him when he flew. In about fifteen minutes, 1F was again at the food when 2F arrived. 1F bill-pointed and the other female flew.

April 28, at 9:05 a.m., 1F, who was alone at the feeding place, rattled and quivered her wings. During the four minutes following this, she turned clockwise gradually, raising her head to send the rattle in all directions, until 2M joined her. As they fed together he bowed. They flew off when a Mourning Dove arrived.

The third time I saw copulation in 1944 was shortly before 7:30 a.m. on May 12. 1F arrived in a tree and rattled repeatedly as she puffed her plumage. Her mate (2M) arrived. The two flew down to the driveway. As he walked to her, she rattled, quivering her wings. He mounted, then moved in a semicircle about her, bowing lightly and making a motion as if to mount again. She repulsed him with the peck-gesture, although quivering her wings slightly. They flew to the feeding plot where she again quivered her wings. An arriving male, greeted by 2M with a low elaborate intimidation bow, moved some distance to one side, behaved as if wary, fed briefly, and flew off.

Six times between April 23 and May 12, 1944 I saw 1F quivering her wings when 2M was with her, and the only time I saw her quiver her wings otherwise was an occasion when 2M probably was close at hand. I did not see any other male than 2M direct courtship bows toward 1F after April 8, until May 25 when an unbanded male arrived. This newcomer courted her and other females occasionally until June 23. I saw him direct six bows to her (once also guarding her from 8M, banded April 29, 1944) but in each instance she used the peck-gesture in return.

#### STATUS OF OTHER RESIDENT COWBIRDS

During 92 observations of 2F and 16 of 5F, I never saw either respond to the courtship displays of bowing males. However, by noting the guarding behavior and intimidation displays of their male companions, I gathered some circumstantial evidence as to which males were their mates. Previous to May 4, 2F was courted by 3M and 5M. The latter attacked the domain-holder 2M on April 16 when that usually dominant male joined them. On April 25, 5M





A male Cowbird intimidating another male through bill-pointing. Photographed at Ithaca, New York, by Arthur A. Allen.

bill-pointed 2M and guarded 2F from him. But after the early part of May, 8M was almost certainly her mate. He consistently accompanied her and used intimidation display in her behalf. Of three recorded instances of intimidation, two were directed toward the dominant 2M. It is possible that 8M had associated and mated with 2F elsewhere previous to his first-observed visit to the feeding plot (April 29), or that she took him as her mate at about that time.

Much less is known about 5F. Late in the season, she was the most constant

companion of a male aluminum-banded in some previous year but not re-trapped for identification. The dominant 2M extended more favorable attention to her than he did to 2F. He sometimes intimidated 2F who spent much time in or near the feeding plot.

I do not know whether 3M and 5M secured mates. I think it highly improbable that 3M won any of the females I saw him courting. He spent more days in the area than any other male Cowbird except domain-holder 2M (I saw 3M on 93 occasions), yet he was under almost continuous domination and was nearly always the "extra" male among the groups.

Referring to Cowbird mating, Nice (1937:153) states: "... here on Interpont, with an abundance of Cowbirds, promiscuity prevails just as the older writers maintained." Although my Nashville group mingled freely in social contacts, I found no evidence of promiscuity among the females. My observations in 1945 and 1946 strengthen my belief that Cowbirds are essentially monogamous. I saw copulation only once in each of those seasons and in both instances the participants were the dominant pair of that season.

#### THE QUESTION OF TERRITORY: THE DOMAIN

Cowbirds have shown strong attachment to certain areas, particularly breeding areas. The remarkable homing experiments of Lyon (1935:7) and Fox (1940) prove that a deported bird will return 'home' from a distant point within a short time. Banding records show numerous returns for several years to the breeding area. Records of return for two and three seasons have been published by Laskey (1944) for four females and one male (with several additions since then). Stevens (1944), who lists returns of ten individuals, informs me by letter that five of these were males and five females, and that three of the females returned for three consecutive years. O. M. Bryens has sent me data from his banding station in Michigan showing that of 2982 Cowbirds banded, 150 were retaken, some of them for several years. Nice (1939:81) found that three females spent two years, and that two females spent three years on Interpont (Ohio). Her color-banded Cowbirds ranged within 18-20 acres usually, within 30 acres occasionally. After their disappearance in July, three of her females revisited their breeding area in September and October (1937:154).

Being unable to follow my color-banded birds in the numerous trees and thickets of our neighborhood, I did not learn how far they ranged. I do have information, however, on their territorial behavior about our house. According to Mayr, Tinbergen, Noble, and Nice (Nice, 1943:162), territory is a *defended* area. Although I saw many threats and fights, they did not seem to be in defense of territory and I witnessed no sustained effort to keep males or females out of a pre-empted area. There was much evidence of what I came to regard as sexual jealousy, however, and, particularly early in the season, of strife for dominance. There was no indication of a peck-order similar to that described

by Allee for domestic chickens (Nice, 1943:92) nor of a society comparable to that of the Jackdaw (*Corvus monedula*), a society in which, according to Lorenz (1938:210) "every bird is jealous of his own position, constantly bickering with those that are his direct subordinates, but distinctly tolerant of those that range far below himself."

The ground about our home could be called a Cowbird *domain*, for it was occupied each season by a dominant male and a dominant female, his mate. They alone used this area for pair formation and mating. They did not drive other Cowbirds from food in this domain, and they tolerated Cowbirds of both sexes in social contacts, feeding and flying together with them. I believe the dominant pair showed vestigial territory behavior in intimidating others and keeping the domain for their own in pair formation and mating. This might be classed as 'Type C, mating station only' (Nice, 1943:163), modified by the fact that they did not object to others feeding there.

Friedmann (1929:175) believed that Cowbirds have definite territories. He said: "Not only has the female a definitely marked-off breeding area, but the male has a definite post, entirely comparable to the 'singing tree' that Mousley describes." He described territories of three pairs at Ithaca but stated (p. 177): "All Cowbird territories studied were not quite as definite as these three. On the west shore of Cayuga Lake the Cowbirds were found to merge the extremities of their areas into neighboring ones. . . ." He also stated (p. 177): "The Cowbirds do not make any very spirited attempts to defend their territories and consequently in regions of unusual abundance the territorial factor is much less noticeable. I have never seen Cowbirds fight and their method of defense is restricted to an intimidation display." (This was the bill-pointing gesture.) Nice (1937:154) said: "Although Cowbirds show no impulse to defend a territory, yet they appear much attached to their spring and early summer homes."

#### ACQUIRING THE DOMAIN

At Nashville during the first part of the season in 1944, 1M held the domain about the feeding plot. He was the first Cowbird to arrive that year and he had lived here three years previously. Early in 1944 he was tolerant of other feeders, showing no aversion to any bird. The first of the females to join him, 1F, he courted as they flew and fed together. He first employed intimidation when an arriving male began to display to 1F. Becoming pugnacious, he fought male Cowbirds, showed belligerence to other species, and participated in elaborate intimidation displays, guarding 1F from other males. So far as I could tell, however, she did not choose her mate until nearly two weeks after her arrival. In the meantime, she fed and flew about with various males. In the contests between 1M and other males from April 1 to 8, I was not always able to analyze the motives in their behavior. There seemed to be strife and ceremonies for dominance as well as for the favor of a certain female. There were at least two

other females, but the domain-holder (2M) showed only passing interest in one of them and none at all in the other. Whether the winner acquired dominance first or the mate first is a question.

On April 8 there were triangle and quadrangle ceremonies among the males, and 1F definitely accepted 2M. I saw no further association of 1M and 1F. Although 1M came to the feeding place several times April 9–11, I did not see a female with him, nor did I see him at all after April 11. From April 10 on, 2M dominated the area. His mate, 1F, also participated in intimidation behavior, dominating the females. I recorded 85 intimidation displays by 2M to individual male Cowbirds, 7 to groups of Cowbirds, 9 to a female Cowbird (2F), and 10 to an individual Mourning Dove, Blue Jay (*Cyanocitta cristata*), Grackle, Brown Thrasher, or House Sparrow. Some 30 displays he directed solely toward 3M, who spent more time about the feeding plot than any other male except himself, and each time he displayed before a group, 3M was part of that group. Only occasionally did 3M bow low or bill-point before 2M, and when he did he was apparently attempting to gain the interest of a female. Sometimes he revealed his timidity by feeding hurriedly and warily when 2M threatened him. Usually he stolidly continued his feeding, keeping his distance when 1F was present. The other males that came regularly showed similar acceptance of 2M as a despot (a mild one) over the domain as long as he did not bow to the females with them.

#### SEXUAL JEALOUSY

The following incidents show, I believe, that intimidation gestures and fighting were not in defense of a piece of ground as in territorial behavior, but were purely sexual.

On April 16, when 5M and 2F were the only birds at the feeding place, and were feeding together, 2M arrived. 5M attacked him, but 2M ran to the female, and 5M came between them to guard her. She walked a few feet and the males fed together—amicably so far as I could see. When 2M moved away, 5M followed him. When 2F flew, both males followed her. Similar encounters occurred between 8M and 2M in the presence of 2F when 8M accompanied her, but these did not involve actual attack.

Strange males, when arriving, used intimidation bows to the dominant 2M at first meetings but he bowed deeply in return and they made no further attempt to intimidate him. Strange males displayed to 1F in his absence. On May 25, June 2, and June 25, unbanded males extended the courtship bow and one guarded, but 1F responded by peck-gestures. *I never saw a resident male aside from her own male escorting her, or displaying to her, after she had mated.* On the other hand, 2M was not averse to extending the courtship bow to 5F or accompanying that female in flight.

The only female that displayed in any way on the domain in 1944 was 1F. She used the bill-pointing gesture nine times in intimidating other Cowbirds (eight times to a female, once to an unbanded male). She bowed once to a

female, 5F, when her mate (2M) was showing attention to this bird. She used the peck-gesture 18 times—once to a Towhee, five times to another female Cowbird, eight times to a newly-arrived male Cowbird that bowed to her, and four times to her mate, repulsing his advances. On the day she fought with an unbanded female (June 15), she first attempted intimidation by bill-pointing. With tail elevated, she fed 6 to 12 inches away, but often stopped to bill-point. Then she ran at the intruder. At this point her mate arrived, and she guarded him from the other female by keeping between them, bill-pointing. When the intruding female approached 2M, 1F ran at her, attacking so vigorously that they rolled on the ground and one of them cried out in pain.

I observed one instance of teamwork between the dominant pair in intimidation. My notes (May 6) read: "2M, 8M feeding, 2M bill-pointing, bowing low. Then 2F arrived; she walked toward 2M as she fed, 8M joined them, guarding the female. In a few seconds 8M bowed low to 2M and ran to another feeding spot where 2F soon joined him. Then 2M bill-pointed, drank once, fed, then flew without song, returning immediately with his mate 1F; 2M and 1F pointed bills upward as they walked around the other pair, which flew."

On another occasion, June 19, as the dominant pair fed, 8M arrived, and 2M made numerous low bows as he followed the other male. 8M responded with two low bows. Then 8M's mate, 2F, arrived and 1F bill-pointed on meeting her. 2F circled on foot to join her mate. 1F followed, still bill-pointing. Then all fed walking abreast, the two males in the center, each male thus guarding his mate from the other male. A few more displays by the dominant pair put the 8M-2F pair to flight. The dominant pair followed. Presently all four birds returned, fed together for a while, and flew off again in the same order.

Drouth in 1944 caused a serious food and water shortage for wild life by the last of June, the end of the Cowbirds' breeding season. Despite the abundance of millet seed and water near my home, the Cowbirds followed their usual custom and departed. The adults began to disappear in early July and all had gone by the 15th. None reappeared at the banding station that year. I seldom see adult Cowbirds near Nashville between mid-July and flocking time in September.

#### THE DOMAIN HOLDER AND DOMINANT FEMALE AS MATES

What I observed in 1945 seemed to indicate that the dominant male mated with the dominant female of the same area. How this came about I could not be sure. To me it appeared that the female which was successful in gaining dominance among females in an area of her own choosing accepted the dominant male of that same area as her mate. In 1945, as in 1944, the dominant male was 2M. Early that spring two females had frequented the banding station—5F, a resident of previous years, and a new arrival, 7F, banded and named on March 27. I saw 2M with both of these females from time to time but did not for some weeks observe anything indicating that he had mated with either.

On April 9 at 7:45 a.m., 2M arrived at the feeding plot with an unbanded female. This female I caught and banded, naming her 8F. As she fed, 8M directed courtship bows and Song 1 to her several times, but received no response. When 7F arrived, 8F attacked her; but when 2M flew off the two females remained to feed. About two minutes later, 2M returned. In what appeared to me to be a pugnacious manner, he attacked 7F, twice on the ground, once in the air, driving her off a short distance. Twice, during these encounters, she used the rattle. She returned immediately after each attack. When 2M left the feeding place again, 7F began bill-pointing 8F, following her over the feeding plot and into the adjoining flower bed. When 2M returned, 7F was some distance from 8F. Having directed a courtship bow to 8F, he left. Presently the two females flew off together. Later that day I saw 2M and 8F together at least twice; he bowed to her but she ignored him.

On April 10, I saw 2M and 8F again at the feeding plot. He apparently was courting her. After his departure from the plot when 7F arrived, 8F started to bill-point her. The two females used this gesture in trees and on the ground for a considerable period, apparently trying to intimidate each other; but 8F gradually became less aggressive and more wary, and later in the day I noted that *it was 7F who followed 2M in flights from the feeding plot*—a characteristic of the female of the dominant pair. I did not see 8F after that day. 7F became the dominant female, the mate of 2M. This position she held until her death on May 20. 2M had no mate after that in 1945.

In 1946, 2M was the first Cowbird to arrive. He came on March 11 and was dominant over other males until March 29. On that date 4M, a visitor of 1944 and 1945, appeared, accompanied by the first female of the season, an unbanded individual. She showed pugnacity that first day by using the peck-gesture to a male Cardinal and later, as other female Cowbirds arrived, she displayed to them with bill-points and peck-gestures. I banded her on April 1 calling her 9F. She was the mate of 4M. From that date, 2M began to lose position as head of the domain. 4M assumed the dominant place, using intimidation gestures toward 2M and other males with no retaliation from them. Although 2M remained as a resident for the season, I saw him less and less frequently and never with a mate. This seems to be further proof that holding the dominant position among males is closely linked with acquiring the dominant female as a mate.

To summarize: in 1944, the dominant position of the first arrival, 1M (a resident of previous years) was forfeited when the dominant female rejected him in favor of 2M, a male which gained dominance among males. In 1945, 2M retained the domain and acquired the dominant female, 7F, as his mate, although he apparently had preferred 8F. In 1946, 2M arrived first but lost the domain to 4M, who had been there as a visitor in the two previous years, and who had as his mate 9F, the dominant female of 1946.

EGG-LAYING

The first Cowbird egg that I found in 1944 was laid in a Cardinal nest on April 23. On the morning of the previous day I had noticed an excited group of Cowbirds (including 2M, 5M, and 1F) above this nest, and had seen 2M attack 5M there. The third Cardinal egg of the set had been laid April 22. On the 23rd this third Cardinal egg was missing and the Cowbird egg was in its place.

On April 26, at 9:00 a.m., I saw a female Cowbird emerge from a dense shrub border at the rear of our place, a hundred feet from the Cardinal's nest. Investigating, I found a Towhee's nest two and a half feet above the ground. In it were three eggs (one pierced), and on the ground below was another (cracked). All these eggs appeared to be Cowbird eggs. I did not see the owner of the nest. I removed the damaged eggs. At 10:30 I found the two eggs in the nest damaged—one pierced, the other broken. The following day I saw a female Cowbird there again. That day the Cardinal nest was empty, and I found a Cardinal egg (somewhat incubated) in the shrub border near the ravaged Towhee nest.

I captured 1F repeatedly in 1944, recording her weight 15 times from March 28 to June 25 (see Table 1). In general, she weighed somewhat less than 40

TABLE 1  
WEIGHTS OF DOMINANT FEMALE 1F

1944	Morning	Grams	Afternoon	Grams
March 28			1:45	37.2
April 3	8:00	35.5		
12	7:00	36.7		
23			3:00	42.4
29			1:00	40.4
30	7:15	38.9	7:15	41.8
May 6	10:30	38.7		
9			2:00	38.8
18	11:45	40.1	6:30	41.9
25	7:00	37.9		
June 10	10:30	40.6		
22			2:00	38.9
25	7:00	36.7		

grams. But on April 23, April 29, April 30, May 18, and June 10 she weighed *over* 40 grams. These dates may well represent also her egg production periods. In any event, the findings tend to corroborate Nice's theory (1937:155 and 1942:89) that Cowbirds usually laid three sets of eggs per season in Ohio.

The weight of 6F on April 29, 1944 was 41.4 grams. Two recorded weights for her in previous years were 39.3 and 40 grams.

On the morning of May 6, 1944, 2F weighed 41 grams. She was probably in or near egg production at that time, for her average morning weight otherwise (4 records) was 39.5 grams. On May 9 and again on May 10, a Cowbird egg was laid in a White-eyed Vireo (*Vireo griseus*) nest in a shrubby border about a hundred feet east of the Towhee nest. This nest was also on 1F's domain, but I do not know which Cowbird laid the eggs. The eggs were not alike in markings and may have been laid by two females.

It is possible that, early in the season when host nests are scarce, two or more pairs of Cowbirds contend for "possession" of these nests. Most certainly there were contentions of some sort in the vicinity of the above-referred-to Cardinal and Towhee nests in 1944. When two or more female Cowbirds are ready to lay, it seems quite plausible that such rivalry should arise, that nests could be filled with Cowbird eggs, and that rival Cowbirds could destroy each other's eggs. My notes concerning the group of Cowbirds seen April 22 near the Cardinal's nest read as follows: "At least 3 males and 3 females were in great commotion in the rear section where all Cowbird eggs were found. 8:40-8:49 a.m. a pair flew to the dense growth of shrubbery and vines, some 30 feet south of the feeding place, under a large silver maple tree. This pair was followed by a male and another pair. Then a female perched for some time in another maple, some 20 feet from the first, over an exposed Mourning Dove nest (bird incubating). A few minutes later, 5M and a right-banded female perched in the first maple over an exposed Cardinal nest (set just completed). The male flew, leaving the female alone. Female 1F arrived in the tree, followed by 5F and a right-banded male: 1F landed near the end of a branch with some males crowding close, 5M nearest to her. He bowed. Then in a swift flight, a male, thought to be 2M, came and attacked the males nearest 1F. All flew to the east side of the lot, lost to sight in the dense growth. Excitement continued for the rest of the morning back there."

Through the 1944 season I put up dummy nests of several sorts, placing in them Bluebird (*Sialia sialis*) eggs from deserted nests and marked House Sparrow eggs. These eggs disappeared, but no Cowbird eggs were laid in the nests.

In 1945 I found Cowbird eggs in seven of nine Towhee nests in which eggs were laid in April and May. An early Towhee nest (eggs laid in March) was not parasitized. The earliest Cowbird eggs of that season I found April 6 (an egg in each of two nests, each egg laid April 4-6).

In mid-May of 1945 I noted much contention among the Cowbirds of the neighborhood. On May 16, I observed that the dominant 2M was limping. That morning there had been bowing ceremonies between him and two other resident males, 8M and 12M. Late that day his leg or foot trouble seemed aggravated, he sometimes lost his balance while feeding, and the plumage of his back was disarranged, the gray basal color showing as if some feathers had been lost. On May 17, an unbanded male spent considerable time at the feed-



ing plot. He and 2M participated in bowing displays to each other at their early meetings, but by evening 2M was doing all of the bowing. At 6:48 p.m. he directed eleven bows to the stranger and, a few minutes later, ten bows while he guarded his mate, 7F. The unbanded male made no response at all.

Early in the morning on May 18 a Cowbird egg was deposited in a Towhee nest in shrubbery near the feeding plot. The domain-holder, 7F, was in egg-production at that time. Early that afternoon 7F arrived at the feeding plot with her mate and an unidentified male. She appeared to be in normal condition then, but at 7:00 p.m., as she flew to a tree near by, I saw that she was tail-less, and when she alighted her posture was that of a sick or injured bird. She remained until 7:20, flying north, probably to the usual roosting place (all Cowbirds flew in that direction at dusk). The following day she made some effort to eat, but stood or squatted idly most of the time. At 7:39 p.m., when a Blue Jay annoyed her, she made a short flight toward the north, but dropped to the ground among some plants. Apparently this was her last flight. I did not see her again, and on the following afternoon (May 20), I searched among the plants, finding her intact body. She probably had died a very short time previously for ants had not yet attacked her eyes. She was thin, weighing only 36.4 grams, a low weight for a laying Cowbird. Dissection revealed an egg in the oviduct with the yolk intact but the shell broken. On the large end of the shell was a dark brown spot, bordered with specks of light brown, but the rest of the egg was immaculate. In the ovary were three enlarged yolks of varying sizes and a mass of tiny ova. It is possible that her condition was caused by the attack of a predator or by an automobile collision, but what I had actually observed the preceding few days led me to suspect that the Cowbirds themselves were responsible. The injuries of her mate and the behavior of the other males furnished circumstantial evidence that fighting involving the 2M-7F pair had been savage.

#### SUMMARY

Through the breeding seasons of 1944, 1945, and 1946, at my home in Nashville, Tennessee, I studied the mating habits and territorial behavior of the Cowbird (*Molothrus ater*). My observations were principally of 29 color-banded individuals (18 males and 11 females), some of which lived about my home for two to four seasons.

Upon their arrival in spring, male Cowbirds indulged in elaborate bowing ceremonies, intimidation gestures, pursuits and fights, striving for dominance among themselves. These activities were connected more or less directly with mating. Intimidation gestures and fights of a similar sort occurred among females also. Bows extended in courtship or greeting by males to females were of various sorts, but none was as elaborate as that given by the male in intimidating another male.

One male became dominant among males, one female among females. I ob-

served copulation one to three times a season between these two dominant individuals, and I observed no other copulation. I did not ascertain whether the male acquired his domain first and then his mate, or vice versa, or whether the dominant female first selected her domain and then accepted as her mate any male which proved to be dominant in that particular area. My observations furnish greatest support for the last-stated theory.

The dominant pair held their dominance through the same intimidation displays as those practiced among the group early in the season. Most important of these in the male were the very elaborate "toppling forward" type of bow, the peck-gesture, the pointing upward of the bill, and the guarding of the female by moving quickly between her and another male. The female maintained dominance over other females by bill-pointing, peck-gestures, bowing (rarely), and guarding her mate from another female. Female display occurred less often than male display. With both sexes, intimidation gestures occasionally ended in a fight. Sexual jealousy was evident.

All of my observations indicated that the species was monogamous, although a number of individuals of both sexes mingled freely throughout the breeding season, feeding and flying about together.

I observed no evidence of true territorial behavior: no boundary lines were defended, and no Cowbirds were excluded from any area. The area (exact size undetermined) occupied by the dominant pair I have here designated as the *domain* because it was used as a mating station by the dominant male and dominant female exclusively.

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