

EXPERIMENTS ON THE MATING BEHAVIOR OF THE BREWER BLACKBIRD

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Under favorable circumstances the social and sexual responses of unconfined and undomesticated birds can be subjected to experimental analysis. The excellent review by Tinbergen (1948) lists some outstanding papers dealing with this topic. Noble (1936) and Noble and Vogt (1935) demonstrated the importance of visual clues in the reproductive activities of wild birds, and the experiments of Lack (1943) in his intensive study of the Robin (*Erithacus rubecula*) illustrate the value of concentrating on the behavior of one well known form. The interest and importance of these and similar studies led us to select a single avian species for an investigation of mating behavior.

MATERIALS AND METHODS

For this investigation, we sought a species which would lend itself to an experimental study under natural conditions. The Brewer Blackbird (*Euphagus cyanocephalus*) was selected as it has marked sexual dimorphism in color, it has colonial nesting habits which make many individuals available in a small area, and on the campus of the University of California, Los Angeles, it is abundant and extremely tame.

We prepared stuffed specimens of both sexes in approximately life-like form; these specimens are referred to throughout this paper as dummies. For our experiments, we placed the dummies on the ground and in the open near various concentrations of blackbirds on the U.C.L.A. campus. After the birds reacted to a dummy once or twice, it had to be removed for about 20 minutes or transferred to a different group in order to obtain more responses. As these birds are thoroughly conditioned to the presence of humans, we were able to make observations at close range without causing any perceptible disturbance.

To investigate the factors which influence mating reactions, we modified the dummies by deletion and substitution of parts and by changes in posture. Cracker crumbs were scattered on the ground to attract the birds' attention to the dummies, but this inducement often proved unnecessary. Experiments were carried out from March 24, 1951, to June 2, 1951.

RESPONSES

The dummies called forth a variety of responses, as described below. Insofar as possible we have employed the terminology used by Williams (1952) in his detailed observational study of the breeding behavior of the Brewer Blackbird.

Display with or without vocalization.—This performance is described by Williams as the "ruff-out." It is very similar in both sexes, but is given more often by the male. In displaying, the bird points the bill upward, fluffs out the feathers of the breast, and spreads those of the wings and tail. The tail is also depressed so that its tip almost touches the ground. Usually a single ascending, half-whistled *squeee* is uttered at the height of the display.

Males may give a display similar to that described above while walking back and forth next to an intended mate. In this display, called by Williams "male pre-coital," the wings are half-spread and drooped slightly so that their tips may touch the ground, and the bill is pointed slightly downward.

We found that in responses of males to dummies, the "ruff-out" and "male pre-coital" displays merged imperceptibly. Immediately prior to copulation with a dummy, the males often gave only a momentary display which we could not distinguish

from the "ruff-out." For these reasons we shall refer to all male display given just prior to copulation simply as "display."

Male elevated-tail display.—This display resembles somewhat the begging action of a young bird. The wings quiver and droop slightly, the head is held horizontal or slightly elevated, the tail is raised to an angle of about 45 degrees, and a chattering call is given. The elevated-tail display is very similar to the "female generalized display" and the "female pre-coital display" described by Williams (1952).

Attempted intimidation by the male.—When the male attempts intimidation he may use the "head-up" display. The feathers of the body, wings, and tail are not noticeably fluffed out or spread. The bird walks stiffly, and the head is raised so that the bill points vertically. In this posture the glossy feathers of the throat and breast are prominent, and these parts are directed toward the adversary. Often additional emphasis is provided by a slight rotation back and forth of the head. No vocalization accompanies this display.

Scolding by the female.—In scolding, the female faces the object or activity which disturbs it and chatters loudly.

Incomplete copulation by the male.—An incomplete copulation is defined here as one in which the male mounts the dummy and goes through the motions of copulation but does not deposit semen. In this definition, "incomplete" refers only to the failure to ejaculate and does not imply lack of vigor in the mating attempt.

Completed copulation by the male.—In a completed copulation semen is deposited on the dummy.

Approach with interest.—We assumed that a bird was interested in the dummy if the bird flew or walked directly toward it to within three feet or less. If no response other than the initial approach was forthcoming, the approaching bird almost always stopped before getting closer than three feet. Interested males frequently advanced toward a dummy so rapidly that they bore a comic resemblance to a person walking as fast as possible without breaking into a run.

Complete indifference.—When the birds paid no more attention to the dummy than to any other inanimate object of similar size, we considered them completely indifferent.

Avoidance.—Often the birds seemed wary of a dummy, and either would not approach it or would alter their direction to avoid it.

EXPERIMENTAL RESULTS

The first experiments were attempted on March 24, 1951, at which time a female dummy was placed near a flock of male and female blackbirds with immediate positive results. From this date through May 8, suitable dummies invariably elicited vigorous responses from the birds. After May 19, with a few exceptions which will be discussed subsequently, the dummies were treated with indifference. The experiments were terminated on June 2, 1951.

The reactions to the various dummies were tested repeatedly; for purposes of documentation, however, we shall cite from our field notes only one or two typical instances of each type of response. Each of these citations is prefaced by the date of the observation, and the form of the original notes has been altered slightly in the interest of narrative continuity.

To simulate the female pre-coital posture, we elevated both the head and tail of a female dummy to about 45 degrees above horizontal (fig. 1). During the height of the breeding season of the blackbirds, this dummy always evoked displays and attempted copulations by the males. Once this had been established, we attempted by selective

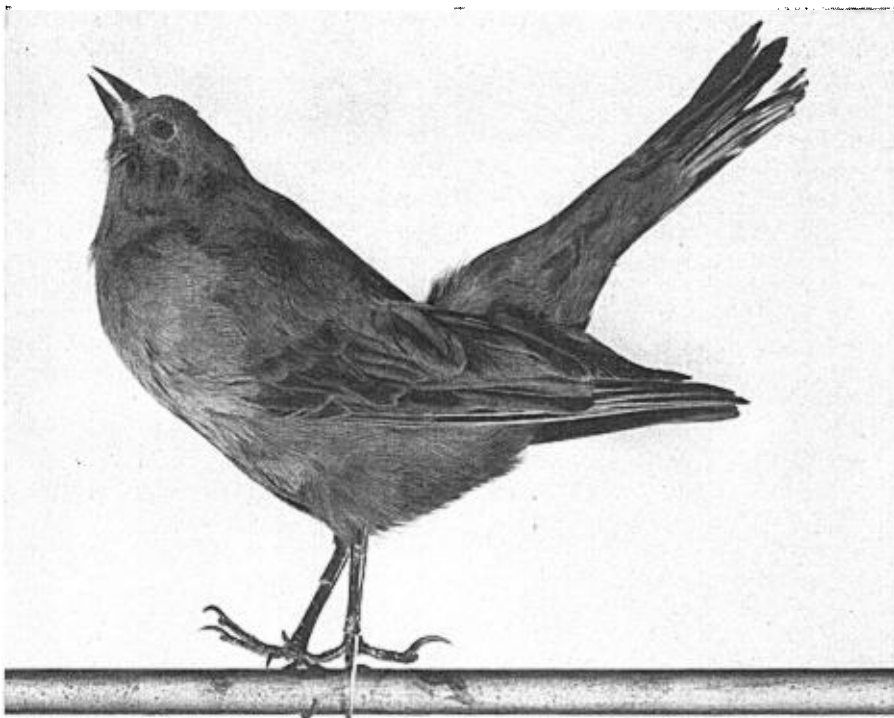


Fig. 1. Dummy of female Brewer Blackbird in copulatory posture.

removal of parts of the dummy to determine the minimal image necessary to induce the copulatory response of the male.

FORM

First we removed the head and neck of a female dummy and found that males copulated with it as readily as if it were intact (fig. 2).

April 7.—As soon as the dummy was placed on the ground a male flew up, alighted about four feet in front of it, walked forward with obvious interest, displayed once at its right front, and mounted. The dummy tilted forward and dislodged him. He walked to its left, mounted the tilted dummy, and a complete copulation ensued. A photomicrograph of a smear of the semen deposited on the dummy is shown in figure 3.

The responses of the males to a female dummy with head and tail elevated but with the wings removed were also the same as to an intact dummy.

May 5.—A few minutes after the wingless dummy was set out, a male approached, mounted, performed a completed copulation, dismounted, and displayed on either side at the rear of the dummy before losing interest.

A female dummy was further reduced by removing the anterior part so that only the tail, the legs, and the posterior two-thirds of the body remained. As a rule the birds were indifferent to this dummy, but males occasionally approached it with interest.

April 14.—This dummy was set up near a male, and crumbs were scattered nearby. The male approached rapidly to within about three feet, then shied away and picked at crumbs. A female flew up, alighted about two feet in front of the dummy, and seemed puzzled and wary. More crumbs were scattered. The male showed a revival of interest in the dummy. He walked toward it from behind, but shied away when he got closer than about three feet. He walked to the front of it, looked, then kept on walking.



Fig. 2. Male Brewer Blackbird copulating with headless female dummy.

Similar results were obtained with other birds, but once an abortive attempt at copulation was made.

May 8.—The dummy was set up near a pair of blackbirds feeding on a lawn, and crumbs were scattered. The male walked toward the dummy but stopped five or six feet away to get a large crumb. Then a male in flight fifty yards away headed toward the pair and the dummy. He braked himself in the air above the dummy, alighted 18 inches behind it, and in one hop mounted it lightly for an instant. Immediately, the male of the pair already present made a sudden aggressive movement toward

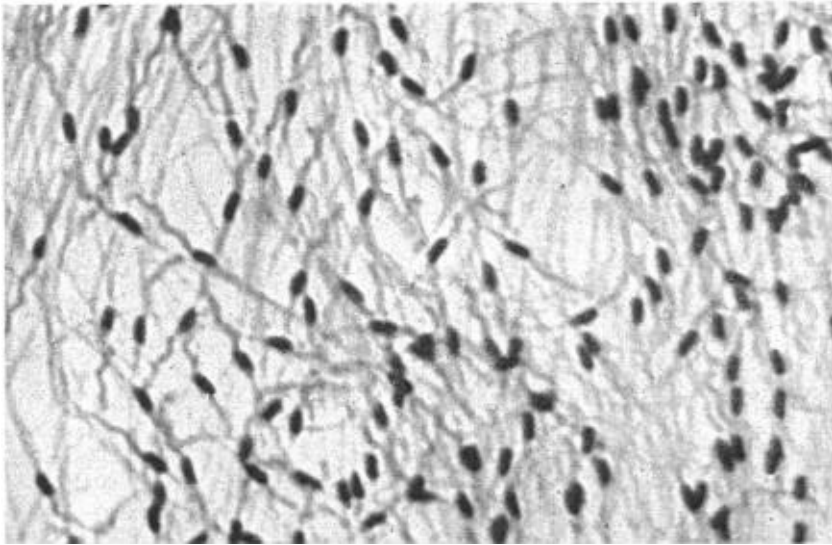


Fig. 3. Photomicrograph of smear of semen deposited on a dummy by a male blackbird, showing numerous spermatozoa; $\times 1150$.

the new male, and the latter hopped off at once without fully attempting a copulation, but his response to the dummy was decidedly positive.

In this dummy, reduction of the anterior parts had evidently been carried to a limit beyond which no reproductive response could normally be obtained. We then began to reduce a dummy from the posterior end.

Removal of half the tail of an otherwise intact dummy did not inhibit the copulatory response of the males.

May 6.—About a minute after this dummy was set out, a pair of blackbirds which were nesting in a vine 15 feet from the dummy flew over from about 20 yards away. The female went straight to the vine, but the male alighted about three feet behind the dummy, walked to it, displayed once behind it, mounted, and twice copulated incompletely without dismounting.

When the entire tail was removed, various responses were obtained from different males.

May 6.—A pair of blackbirds flew up to the dummy. The male hovered about three feet above it, but did not alight. Then another male flew up, alighted three feet behind the dummy, watched it, but did not display. Another pair alighted near the dummy. The male was behind it and apparently interested, but he did not display. Five minutes later another male alighted about one foot from the dummy, followed by a female which alighted a moment later two or three feet in front of it. This male displayed once behind the dummy, mounted, performed an incomplete copulation, dismounted, and displayed while pacing back and forth behind it.

The dummy was then altered by removing the wings, leaving only the head, body, and legs. This greatly reduced form likewise called forth various responses.

May 8.—The dummy was set out near two pairs of blackbirds. For about five minutes they showed no interest. Then one pair flew to within 15 feet of the dummy. The male walked to within about 10 feet, looked at it, then walked toward it rapidly with apparent interest. The female, however, walked even faster, passed him, and seized a crumb about three feet from the dummy; the male veered to the side and did not approach again.

The dummy was then placed in another area. After two or three minutes two pairs came within four feet of it; the birds showed no response.

The basal half of the tail was then replaced on the dummy. In about a minute, a male alighted three feet from the dummy, walked rapidly to its front, displayed once, and mounted. The dummy fell on its side; the male continued displaying behind it but did not remount.

The half-tail was again removed and the dummy set up 25 feet away. Soon a pair came to within five feet of it, the female in the lead. The male walked within two feet of the front of the dummy, eyed it, but then flew away after the live female. A moment later a male glided up from at least 30 feet away, alighted about five feet from the dummy, walked to its front, displayed once, and mounted it. Just as he seemed to get well settled on the dummy it fell over. The copulation was not completed.

It seems evident from the mixture of positive and negative responses that the wingless, tailless dummy had been reduced posteriorly to the minimal image which would evoke a mating response.

POSTURE

Our next series of experiments consisted of altering the posture of the dummy. Since a female dummy in the normal position of the mating bird, with the tail elevated, invariably evokes a copulatory response from a male in breeding condition, we first bent the tail of a female dummy downward to about 30 degrees below horizontal. In all other respects this dummy approximated the usual mating posture of the female blackbird.

May 5.—The dummy was set out on a lawn, and three pairs of blackbirds came up immediately. A male approached the dummy from the rear and paced back and forth giving a half-display. The other birds gathered around chattering; some were picking at crumbs but all obviously noticed the dummy. Another male approached from behind, paced back and forth within 18 inches of the dummy, but did not display or mount.

The dummy was then set out nearby, with the tail now in a horizontal position, and mixed results were obtained. One male flew up and hovered over the dummy but did not alight. Ten minutes later a male glided over, alighted one foot from the dummy, displayed at its left front, mounted, dismounted, displayed on either side at the rear of the dummy, but did not remount. The copulation was incomplete. The dummy was moved away about 20 feet. Three pairs were soon attracted, and one male approached it from the side with obvious interest. As he got within two feet, another male displayed and made a short rush, driving the first one away from the dummy. Then a male approached the dummy from the rear and to one side, paced back and forth, but did not display.

The tail of the same dummy was then elevated to about 15 degrees above horizontal. As soon

as the dummy was placed on the ground, a male standing 18 feet away walked rapidly and directly to it from the right front, displayed twice on the way, displayed once beside it, and mounted. The dummy fell over, but the male displayed and mounted three times more. At least one of these copulations was completed.

These results indicate that the angle at which the tail is held is a very important postural element in stimulating a mating response. An immediate positive response is forthcoming only when the tail of the dummy is elevated above the horizontal. It is perhaps significant that in the begging posture of the juvenile, which closely resembles the copulatory position of the adult female, the tail is held approximately parallel to the ground.

COLOR

The marked color dimorphism of the Brewer Blackbird suggests that visual stimuli are important in the mating behavior of this species. The iris of the male is pale yellow whereas that of the female is dark brown. The plumage of the male is glossy black with a purple sheen, especially on the head, neck, and breast, and that of the female is dull grayish brown shading to black on the wings and tail. Composite dummies, combining both male and female parts, were used to test the significance of these color differences.

A yellow-eyed male dummy in the female copulatory posture evoked avoidance or intimidation; it never called forth a mating response from other males. Females showed wariness or indifference.

March 25.—A male dummy as described above was set out. Soon a male came to a low branch above the dummy, looked at it for about two minutes, and then descended to the ground about three feet in front of it. He walked toward the dummy, gave a "head-up" intimidation display while walking, seized a crumb, and flew off.

March 27.—The same male dummy in the same pose was set out. A female started feeding about three feet from the dummy but came no closer. A male came and fed three or four feet behind the dummy. Another male approached the dummy from the front and went into a partial "head-up" intimidation display. He continued forward slowly to within two feet of the dummy, warily grabbed a crumb, and retreated.

To investigate the importance of eye color in sexual behavior, we darkened the eyes of a male dummy with black ink. This caused no change in the response of either sex to the dummy.

April 1.—Soon after the dummy was set out, a few males and females came to within two or three feet of it but were decidedly wary. Crumbs were tossed nearby; a male flew over, started to alight, saw the dummy, altered direction, and fluttered away.

Similarly, yellow eyes did not affect the copulatory response of the males, for when we placed yellow eyes in a female dummy, males copulated with it repeatedly (fig. 4).

March 25.—A male flew up to the yellow-eyed female dummy, displayed once in front and to one side of it, mounted, attempted to copulate, dismounted, displayed again in front, and mounted again. Then another male flew up, chased the first one away, returned to the dummy, displayed, and mounted. He dismounted, displayed twice, mounted, dismounted, and displayed while walking back and forth before the dummy. For a few moments he perched crosswise on the dummy and pecked at the base of its tail. All of the copulations were incomplete.

Despite the conspicuous sex difference in eye color, the mating response of the male is evidently not inhibited by yellow eyes.

The importance of plumage color was tested next. A dummy with a female body, wings, and tail but with a male head, neck, and breast evoked a complicated pattern of response from the males.

April 11.—A dummy as described above was set out and food scattered around it. Three males and two females approached from the front, but none came closer than six feet. All looked at the dummy and seemed wary; none came up for food.

April 14.—The same dummy was set out, and for a few minutes no blackbirds were in sight. A

lone male in flight swooped down over the dummy, hovered for a moment, and flew off. Then, after five minutes, the male of a pair in flight at least 75 feet away swerved and headed for the dummy; the female followed. The male alighted directly on the back of the dummy, started to copulate, looked down and seemed suddenly disturbed, hopped into the air, and thereby knocked over the dummy. He looked at it from the side and gave it an aggressive peck on the head. His mate had meanwhile remained about six feet behind, chattering. Two other pairs flew up and hovered above the fallen dummy, chattering. Another male then flew to the dummy from behind, alighted on the ground, walked to it, and mounted. Almost as soon as he got on he hopped off to one side, looked at it, mounted, and dismounted again. Then he walked to the right front of the dummy, seemed about to display, but did not. Again he quickly mounted and dismounted, gave the start of a display, and then nervously snatched a crumb and flew to a nearby perch. None of the copulations was completed.



Fig. 4. Male Brewer Blackbird copulating with yellow-eyed female dummy.

The male portions of this dummy seemed definitely to inhibit the mating responses of the males as soon as those parts were noticed.

The reciprocal of this last dummy was made by placing a female head and neck on a male body, wings, and tail. Again a complex pattern of response was obtained.

May 5.—The male dummy with the female head and neck was set out. A male came up to it curiously but merely picked at crumbs nearby. Another male glided up from the right front, alighted, walked to the dummy, seemed about to display, but hopped back. He walked toward it a little more from the rear but again hopped away in an agitated manner. He then lost interest in the dummy and began picking at crumbs.

April 17.—The same dummy as above was set out and crumbs scattered near it. A pair of blackbirds walked toward it, but seemed wary even though its front faced them; they came no closer than three feet. Another pair flew up, hovered two feet above it, and backed off two feet before alighting and feeding. A third pair walked up to it and fed within two feet of the dummy.

In a nearby area several blackbirds were assembled, and a female was giving elevated-tail displays before two males. The male closest to her successfully intimidated the other male with a "head-up" display but made no attempt to mate with the female. Instead, he remained in his intimidation pose for about 30 seconds while she stopped displaying and walked away. Then the dummy was put down 10 feet away with its front facing these birds, and the "dominant" male immediately walked toward it with extreme rapidity. When about 18 inches from the dummy he stopped, gave a little jump upward and slightly backward, and then continued on. He displayed at the left front of the dummy and mounted; the dummy tilted forward and dislodged him. He mounted six more times. In between these attempted copulations he paced back and forth at the right of the dummy, giving continuous displays including a few of the elevated-tail type. None of the copulations was complete.

Apparently this male was in such an excited condition that his sexual impetus was enough to overcome the moment of hesitancy which almost halted him 18 inches from his intended "mate." No other birds attempted to copulate with this dummy.

SEASONAL DIFFERENCES IN RESPONSES

In view of the many immediate responses cited above, the failure of the birds to react to dummies late in the spring was striking. On May 19, for example, an intact female dummy in the copulatory position secured only negative results when placed at several localities where blackbirds were abundant. At least four males came within three or four feet of the dummy, but no closer. They showed no interest in it, and came close only to pick at crumbs. At that date most of the birds had young which were almost ready to leave or were already out of the nest. It would have been desirable to collect specimens on campus for histological examination of the gonads, but practical considerations prevented this. All reproductive responses by the birds had not ceased, however, as the following accounts show.

May 30.—An intact female dummy in the copulatory position was set down on a lawn near a group of blackbirds. A male walked up from 25 feet away with apparent curiosity, but came no closer than two or three feet and gave no displays. Then a female crouched, walked to the front and then to the back of the dummy, and gave it a sharp peck in the cloacal region. A minute later several birds of both sexes gathered, but no displays were made although the dummy was clearly a source of interest. They dispersed. Then a male walked over from about 30 feet away, displayed while walking back and forth in front of and behind the dummy, but did not attempt to mount. As he began to walk away, a female with food in her beak alighted behind the dummy and walked toward it, possibly mistaking it for a large begging juvenile. She stopped about 18 inches away, still behind it, and watched for about a minute before flying off. A male flew up from at least 40 feet away, alighted beside the dummy, displayed twice while walking back and forth beside it, and mounted. Two other males came up on either side next to the dummy but did nothing further. The male dismounted, and all the birds dispersed. About a minute later, a bird with dark eyes and female-type plumage walked to the dummy and mounted it. The dummy tilted forward, and the copulating bird pecked gently at the crown two or three times. Several birds of both sexes gathered around; the one attempting to mate dismounted and stood quietly beside the dummy for a few minutes. Then all the birds dispersed. None of the copulations was completed.

The bird just discussed might have been a female, but far more probably it was a juvenal male. Young males are not readily distinguishable from females until after the first molt.

Three days later a similar response was obtained, perhaps involving some of the same birds, as the locale was only 20 yards from that of the experiment of May 30.

June 2.—The same dummy in the same posture was set out. Two juveniles on the ground about 15 yards away were being fed by an adult male. The dummy seemed to attract attention at first, for several females and two adult males, including the one which was feeding young, approached. None, however, showed any sexual interest in the dummy, and they soon went away. About five minutes later, an adult male flew to the dummy from a tree about 30 yards away. He walked back

and forth at its right rear, displayed without vocalizing, and mounted. He dismounted, displayed again, this time with a clear *squeee* and remounted. This was repeated twice more. After mounting and dismounting a fourth time, he remained standing two feet from the dummy and seemed to rest. In another minute he flew away. A few minutes later an adult male came up from the same direction in which the previous one had gone; it may have been the same bird. He alighted about two feet from the dummy at the right rear, displayed once, but did not go closer immediately. A moment later, a bird with dark eyes, female-type plumage, and a tail shorter than that of an adult came up to the dummy also. This bird, probably a young male, stood by while the adult male mounted the dummy. The adult dismounted, and the juvenile mounted almost immediately, without displaying. Then the young one dismounted and the adult male again attempted to copulate. After the adult dismounted the young one tried to copulate twice more. Then both stood beside the dummy, panting. The copulation attempts were all incomplete. First the adult and then the young bird departed. Meanwhile, the adult male which was feeding two juveniles went on making regular trips to and from them with food, paying no attention to the mating activity going on less than 15 yards away.

The variety of responses shown by the birds described above indicates that they were in slightly different phases of their reproductive cycles. It seems likely that the young bird was a juvenal male of an early brood; possibly his behavior was an example of social facilitation as defined by Thorpe (1951).

RESPONSES OF THE FEMALE

The responses of the females to the dummies were far less marked than those of the males and typically consisted of indifference or slight fear. In one instance a female gave a "ruff-out" display within two feet of a male dummy, but since live males were in the immediate vicinity the display may have been addressed to them.

Many of the malēs whose activities have been described above were paired with females, and when a male responded to a female dummy, his mate often showed great agitation and scolded vigorously. As previously described, a female once actually struck a dummy, and another female approached one as if to feed it.

GROUP RESPONSES

Both males and females frequently responded as a group to the efforts of a male to copulate with a dummy. In this behavior pattern, virtually all the blackbirds within sight of the mating "pair" gathered in a group around them. The first birds to arrive started a continuous chattering which seemed to attract any others within earshot; they too flew over and joined in the vocalizing. All the onlooking birds oriented toward the "pair" and bobbed up and down slightly. Often one or more birds of either sex gave displays of either the "ruff-out" or "elevated-tail" type or both, but we never saw these lead to an actual mating. Two examples of this behavior pattern are given below.

March 25.—Two males were intent on mating with a female dummy; one intimidated the other, displayed, and mounted the inanimate female. As he was doing this, a female flew into the lower branches of a tree about 12 feet away and chattered. Within 15 seconds five females and a male flew up and alighted within a radius of 15 feet of the dummy and the first male. There were now three males and six females present. The female in the tree gave an elevated-tail display; none of the other birds gave any perceptible response to her. After dismounting, the first male stood quietly about 18 inches from the dummy, and the rest of the birds seemed very alert. Five to seven minutes later the members of the group departed one by one.

April 27.—A male was attempting to mate with a dummy consisting of a male body with a female head and neck, as described on p. 146. During the two minutes that the male was displaying and mounting, five pairs of blackbirds had gathered about, chattering. At least one male in this group gave an elevated-tail display. After the sixth copulation attempt of the mating "pair," one bird sounded two or three clear, whistled *tee-uuu's* and the whole flock took flight in unison and alighted about 20 feet away.

The group response is not stereotyped, but it consistently involves rapid gathering, chattering, orientation toward the mating "pair," and, apparently, sexual excitement. It resembles somewhat the gathering behavior which often occurs when a bird is attacked by a predator or is otherwise in distress, but clearly differs from this in being intraspecific.

RESPONSES TO OTHER SPECIES

Only a few experiments involving interspecific reactions were attempted. For these, dummies of the male Cowbird (*Molothrus ater*), male Red-wing (*Agelaius phoeniceus*), and Hermit Thrush (*Hyllocichla guttata*) were arranged as closely as possible in the mating posture of the female Brewer Blackbird and set out near a flock of the latter species. The male Red-wing was regarded with complete indifference by both sexes. The Hermit Thrush was tested in the hope that it might indicate whether or not any brownish bird in the proper pose would get a response. It, too, was treated with complete indifference by blackbirds of both sexes, but as this dummy was not used until May 12, when responses were beginning to decline, the negative results are possibly not significant.

The male Cowbird, a small icterid with a brownish head and glossy black body, provides an approximate combination of the color characters of both sexes of the Brewer Blackbird. This dummy was set out on April 7, and it received no attention whatsoever. Twice a male blackbird picked up crumbs within six inches of the dummy and gave it no apparent notice. On May 8, a slightly different response was obtained. Less than a minute after the dummy was set out, a male at least 30 feet to the rear flew up, alighted five feet behind it, and walked rapidly toward it. He looked at the dummy with apparent interest for a moment, but gave it no further attention and then walked away. It appears that stuffed specimens of these other species did not approximate closely enough the stimuli provided by a dummy of the Brewer Blackbird itself.

DISCUSSION

Our experiments indicate that the mating behavior of the Brewer Blackbird does not depend on one major factor but on combinations of such elements as form, posture, and color, any one of which is in itself insufficient to evoke a reproductive response.

In this species, as in many other strongly dimorphic birds, visual stimuli are of great importance in mating behavior. Nevertheless, although eye color and plumage color are conspicuously different in the sexes of the Brewer Blackbird, eye color does not seem to affect the sexual behavior of the male, and a few mating responses were obtained by using dummies with high proportions of male-type plumage. Although appropriate posture is necessary to elicit a mating reaction, the response does not depend on posture alone. This is not surprising since both sexes may on occasion display in a virtually identical manner. It is of interest, however, that the minimal requirements of form, posture, and color which call forth mating behavior by the male may be satisfied by a variety of combinations of these elements.

The fact that a male was already paired with a live female did not affect his readiness to respond to the dummy. This may be related to the polygamous habits of the species, which have been demonstrated by Williams (1952).

As the dummy is silent, it is clear that no vocal response from the female is necessary to evoke the mating reaction of the male. Although wing-quivering by the female may be used to attract the attention of the male (Williams, 1952), movement by the female is not necessary, for the dummy is motionless. Indeed, lack of motion seems to be an important factor in evoking copulatory responses in many birds (Tinbergen, 1948:39), and Brewer Blackbirds have been observed attempting to mate with a dead female

which had been shot from a flock (Kenneth E. Stager, Los Angeles County Museum, personal communication).

The dummy was necessarily stationary and silent, but we were able to vary a number of other factors involved in stimulating the mating response of the male blackbird.

Removal of the head of a dummy did not inhibit the mating response, nor did removal of the wings, nor even the wings and half of the tail as well. When the entire tail was removed, however, the males did not respond as readily as to a more complete dummy. When the head, wings, and anterior one-third of the body were removed but the tail left intact, only one bird reacted to the dummy in a positive manner. Apparently the dummy must have enough form to be recognized as a bird and possibly as a particular species, and must be distinguishable as regards anterior and posterior.

Although its presence is not essential to elicit reproductive behavior, the tail is probably the most important feature in mating posture. When depressed below horizontal, it is an inhibiting factor; when horizontal, it calls forth both positive and negative responses. When elevated even slightly above horizontal, however, it rapidly brings on mating behavior.

The position of the dummy becomes less important once the copulatory reaction of the male has started, for males frequently continued their mating attempts with a dummy which had tilted forward or fallen on one side.

The present evidence suggests that eye color is not significant in mating behavior; this does not mean, however, that eye color is not perceived by the birds or that it may not contribute in some way to sex or species recognition. Eye color clearly does not inhibit sexual responses by the male, but the possibility that it might have some effect on the receptivity of the female is untested.

Plumage color strongly affects the reactions of the male. The color of the head, neck, and breast appears to be of greater significance than that of the other parts. Males which mounted a dummy with a female body and male foreparts became puzzled or aggressive as soon as the distinctive glossy black color was perceived. Although it occurred only once, a sexually excited male did give a strong mating response to a dummy with a female head and neck on a male body, wings, and tail. The color of all the parts seems to be significant, but it is not surprising that the color of the foreparts, which are featured prominently in both aggressive and mating displays, should be of particular importance.

Mention should be made of the extraordinary rapidity of some of the responses of the males. At the height of breeding activity, an appropriate dummy often produced a reaction the instant it was perceived. An excellent example is the response, cited on page 146, in which a male in flight changed course at right angles 75 feet from the dummy and alighted directly on the dummy's back. A building prevented the bird from seeing the dummy until the instant before he swerved, and not more than two seconds elapsed between perception and mounting.

Another notable fact, demonstrated on many occasions, is that the reproductive behavior of the male, once it is released, may go to completion even though the sexual "partner" is entirely passive. Contact with the cloaca of the female is unnecessary, for males sometimes deposited semen on the side or flank of the dummy as well as approximately in the cloacal region. Although not necessary to bring about ejaculation by the male, active cooperation by the female must be required for fertilization.

SUMMARY

The Brewer Blackbird (*Euphagus cyanocephalus*), an abundant, sexually dimorphic form, is a favorable subject for experimental study of mating behavior as it re-

sponds readily to stuffed specimens (dummies) of its own species. To test the effects of form, posture, and color on mating responses, we modified dummies by alteration of position and by deletion and substitution of parts of both sexes.

The reactions of females to dummies are largely negative, but males respond vigorously, often mounting the dummy and depositing semen. Both sexes frequently react as a group to the efforts of a male to mate with a dummy. This group response involves rapid gathering, chattering, and orientation toward the mating "pair." Dummies of *Molothrus ater*, *Agelaius phoeniceus* and *Hyalocichla guttata* evoked only passing interest or indifference.

To obtain a mating response from the male, a dummy must meet certain minimum conditions. The wings are not necessary. Either a head or a tail must be present, but one or the other may be removed without eliminating the response. Further removal of parts inhibits the mating reaction. If the tail is present, it should be at an angle above horizontal. Eye color is not important. The plumage color should be predominantly that of a female, but a female head and neck on an otherwise male-colored dummy may be effective when the male is in a state of high sexual excitement. When the dummy presents any one of the appropriate combinations of characteristics, the response of the male may be virtually instantaneous.

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