A BEHAVIOR STUDY OF THE RED-WINGED BLACKBIRD[1]

I. Mating and Nesting Activities

BY ROBERT W. NERO

THIS study is concerned with the behavior of the Red-winged Blackbird or "Redwing" (*Agelaius phoeniceus*) on a breeding ground near Madison, Wisconsin, during the years 1948 through 1953. Part I describes the behavior related to pair formation, courtship and mating activities. The formation, maintenance, size, and structure of the male territory, female territorial behavior, and behavior of first-year (immature) males will be described in a subsequent issue of this journal. The study is a continuation and expansion of a more general study of this species initiated in the same area by James R. Beer in 1945 (Beer and Tibbitts, 1950) and is part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Zoology at the University of Wisconsin (one aspect published previously: Nero and Emlen, 1951).

Grateful acknowledgment is tendered Professor John T. Emlen, Jr., who offered advice and guidance throughout the study. Thanks are due the following persons for aid in various ways: Professors Robert A. McCabe and Joseph J. Hickey; Drs. James R. Beer, Ernst Mayr, Nicholas E. Collias, Ruth L. Hine, Howard Young, Arnold Bakken, Arnold Petersen, Robert L. Strecker, Fred A. Ryser, Frederick Greeley; Mr. Jack Kaspar, Mrs. L. S. Miller, and Miss Margaret Grismer. I wish to give special thanks to my wife, Ruth F. Nero, for her constant support during the years of graduate study. This study was aided by a Louis Agassiz Fuertes Research Grant awarded by the Wilson Ornithological Club in 1952.

Methods

The main study area was a 2.4-acre cattail (*Typha*) marsh on the east shore of Lake Wingra in the University of Wisconsin Arboretum at Madison. This marsh is bordered by red osier dogwood and willow, and is surrounded on three sides by a fairly dense stand of mixed hardwoods. Observations were also made at a feeding and flocking area in Vilas Park Zoo, about one-half mile north of the marsh. Additional records were obtained wherever Redwings were encountered.

Field notes were recorded on 358 days during six breeding seasons, from 1948 through 1953. (Supplementary notes were made in 1954 and 1955.) Observations began each year with the arrival of the first resident males in March and continued until August or September when resident birds (marked) left the area. Most of the photographs were taken by the author

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Male Red-winged Blackbird (*Agelaius phoeniceus*) engaged in "song-spread" display. Photographed by Robert W. Nero, near Madison, Wisconsin, on May 15, 1955.

in April and May, 1955, on several marshes within eight miles of Madison. The photos in Figure 3, however, were taken in July, 1955, in Saskatchewan, Canada, with the aid of Mr. Fred W. Lahrman.

Trapping of adults and immatures was accomplished by means of wire-mesh, treadle-sprung traps baited with white bread. These traps were placed on top of muskrat houses and floating boards, and on top of wire screens which were pressed onto old, standing cattails. Several females were captured by placing a screen-bottomed trap directly on top of the nest when the female had a full set of eggs or young. Individual identification was obtained by the use of combinations of colored plastic "leg" bands. A drop of Duco cement applied within the plastic coil secured the band. From 1948 through 1952, 282 birds were so marked, 175 of these being juveniles. Observations were made with the aid of binoculars from several vantage points within the area as well as along the edge. In 1949 observations were greatly aided by watching from a board fastened between two trees on the edge of the marsh, about 12 feet above the water. This worked so well that in 1950 two towers 12 feet high were erected in the marsh. These elevated platforms permitted close observation of behavior ordinarily concealed by the vegetation.

The Birds

Size of population.—The number of adult males holding territories on the study area during the height of the season (middle of April to middle of June) ranged from about 17 to 25 during the years 1948 through 1953. The number of females with nests during the same period ran from 27 to 50.

Dates of arrival and last appearance.—From 1949 to 1953 previously-resident males (8 to 13 marked males each year) first appeared between March 6 (1950) and March 17 (1952) (average, March 10–11). The last ones to arrive appeared between March 22 (1953) and April 21 (1949). The minimum period for arrival of all the marked residents was 9 days (1953, 9 birds); the maximum, 43 days (1950, 13 birds). The average arrival period was 29.2 days. Certain males were consistently early arrivals, others consistently late. First arrival dates for individuals varied in consecutive years over a period of up to 20 days (average, 13.6 days). Previously-resident females arrived first on April 8 (1952), April 16 (1951), and April 17 (1950). Information on dates of last arrivals of females is available only for 1951, in which year the last marked bird appeared May 7. This gives a period for arrival of females that year of 21 days.

Very few marked birds were seen on the marsh in August, but some were seen on the feeding grounds at Vilas Park during this month. In 1948 a resident female and her young were still on the marsh on August 4;

they appeared to be the last birds present. On August 15 of the same year a marked adult male was seen at the park. A banded young was seen on the marsh on August 6, 1949. Evidence that at least some of the local residents do not migrate until later was obtained in 1951 when two marked adult males were seen on October 22 and 23, respectively, three miles from the breeding marsh. Each male was with a flock of about 50 males.

Annual returns.—Fifty-six per cent of 50 marked adult resident males returned at least once during the period from 1947 to 1953. Each season, from 10 to 22 adult males were present (see Table 1). Marked resident females showed a similar rate of return. Of 48 birds, 56.2 per cent returned at least once during the seasons 1949 to 1953. Table 1 shows the survival of each year's marked population. Of 16 different males, 10 survived five years, three survived six years, and three survived seven years. (Note: two 8 year olds returned in 1954 and a 9 year old bird returned in 1955.) Two females survived at least six years. Some of these birds were banded as adults and may have been older. Davis (1953) reports a life span of 15 years in captivity for the Cuban Redwing, *A. p. assimilis.*

Polygyny.—Polygyny in the Redwing has been recorded by several authors (Allen, 1914:92; Roberts, 1932:306; Linsdale, 1938:140–141; Mayr, 1941:83), although a few observers have reported this species to be

TABLE 1

YEARLY RETURN OF MARKED RESIDENT REDWINGS

The top number in each vertical column is the number of new residents marked that year. Reading down each column one sees the subsequent return of each year's population.

Males

Year	1947	1948	1949	1950	1951	1952	1953	Total Population
1947	11							11
1948	7	10						17
1949	5	5	12					22
1950	2	3	8	7				20
1951	2	2	5	5	7			21
1952	1	1	1	2	3	4		12
1953	0	0	1	2	3	4	0	10

Females

Year	1949	1950	1951	1952	1953	Total Population
1949	15					15
1950	12	32				44
1951	5	14	2			21
1952	2	9	0	0		11
1953	0	9	0	0	0	9

monogamous (Williams, 1940:268; McIlhenny, 1940:85). Redwing matings in this study were occasionally monogamous but were mainly polygynous. Of 25 males for which accurate records were kept, five had one mate each, 16 had two mates each, and four had three mates each. I have no record of a male breeding successfully with more than three females. However, in at least one case where a male had three mates, one female returned for a second nesting, so that four broods were brought off in this territory. Linsdale (*loc. cit.*) working with unmarked birds in Nevada, reported that one male ". . . would have as many as 6 females all actively nesting."

According to Linsdale (*loc. cit.*), "The success of a male in obtaining females in its territory seemed to depend almost entirely upon the suitability of the habitat for nest locations." My females showed a preference for nesting on the edges of the openings within the dense cattail stands. Since not all territories had an equal amount of edge, some might have been more suitable for nesting than others. Linford (1935:37) found that the territories of polygynous Redwing males were twice the size of those of monogamous males, but I found no relationship between territory size and the number of nesting females. In Linford's study, however, the birds obtained the bulk of their food within their territories, whereas my birds obtained most of their food outside their territories.

Allen (1934:136) considered that the male Redwing was not "agreeable" to polygamy because of the great difficulty of running two or three double families each season. He suggested that a male was "satisfied" with one female. However, the males in my study played little part in feeding the young and only a very few birds (three) had more than one brood. Female intolerance of other females may play a large part in limiting the number of females breeding in one territory; a male is rarely able to successfully "court" two females at exactly the same time. Nesting data tend to support this — in most, but not all, cases females within a single male's territory are "out of phase" with each other (see Table 2).

Second nesting.—As Beer and Tibbitts suggested (1950:73) double broods are uncommon in the Redwing in this area. Only three cases of double broods were recorded in this study (in 1949, all successful). In 1950, the year for which the most data are available, 20 marked females had successful first nests, but none of these females returned to the marsh for a second brood. In each case in which females had second broods, they bred with their original mates. A female which arrived on April 17 had fledged young on June 8, and nine days later she had her first egg in her second nest. Another female which left with her young on June 15, returned on June 28 and had her first egg on July 4, seven days later. A third female was feeding her fledged young until June 27 and on June 28 had her first

TABLE 2

NESTING STAGES OF FEMALE HAREM MATES IN SEVEN MALE TERRITORIES ON JUNE 7, 1950

Territory	Female 1	Female 2	Days apart
A	young at 2 days	young at 3 days	1
B	3 eggs	young at 6 days	6
C	3 eggs	young at 5 days	25
D	2 eggs, young at 1 day	young at 4 days	3
E	4 eggs	young at 3 days	12
F	3 eggs	young at 7 days	7
G	4 eggs	2 eggs, young at 2 days	2

egg in her second nest. In two of the above cases the pairs were never separated, the females remaining on or near the territory while feeding the young.

PROMINENT DISPLAYS AND POSTURES

The behavioral characteristics described below include sexual, aggressive, and social posturings. Other sequential displays which are neither as well-defined nor elaborate are discussed under various sections (see Courtship and Copulation). Vocalizations are not completely covered in this study.

Exposed epaulets.—Exposure of the patch of red feathers on the male's wing is a generalized display seen on many occasions, usually in conjunction with other postures or movements. At higher levels of intensity the red coverts may be erected and even vibrated, thus greatly increasing their area and color effect. When a hawk is overhead, when a male trespasses on another territory or is being dominated, or when a male is feeding together with other males on the ground, the red coverts are kept concealed.

Male song-spread.—"Song-spread" designates the behavior of the Redwing during the delivery of the well-known "oak-a-lee" song. Variations of the male display may be seen in Figure 1 (*a*, *b*, *c*, *g*, *h*, *i*). Usually the head is lifted or thrust forward, the tail is spread and lowered, the wings are spread, and the epaulets are raised (see Figure 1*g*, *h*). The head is thrust out with the first note of the song; at the climax, the drawn-out "lee," the tail and wing feathers are carried to the extreme position. The closure of song usually marks the return to normal position, but often the spread display is held for some time afterwards. The extent of song-spread, and other displays, varies with the level of motivation. In extreme or "complete" displays the wing-tips touch the outer tips of the tail, the bird sometimes assuming an almost disk-like form (Fig. 1*h*, *i*). The last phrase of the song is similarly given with varying emphasis. According to Allen (1914: 89) the song ". . . is always accompanied by spreading of the wings and tail feathers and by erection of practically all the body feathers, especially

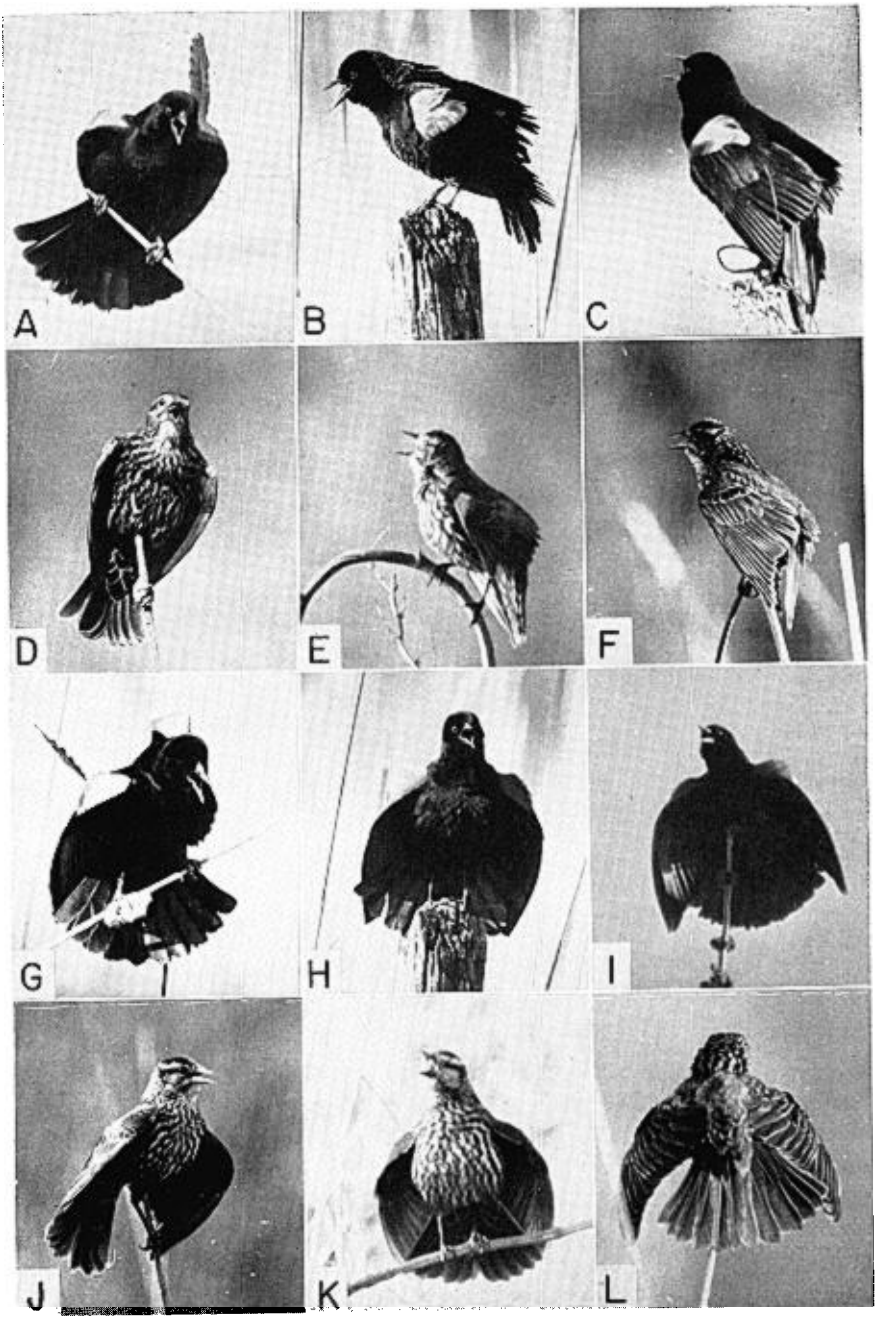
those of the shoulder patches." However, this song is sometimes given with little plumage display (Fig. 1*a*).

Song-spread is given commonly on the territory but it is also frequently given off the territory and before and after the breeding season, though generally without the postural components. Migrating Redwings are in constant song, especially on the roosting grounds. Although song is often given by solitary males, it is given with a greater frequency and extent in the presence of other males. It appears most extensive when directed toward a particular individual. Song is most frequently given while the male is perched but it is also given while in flight. It may at all times, however, be readily distinguished from the "flight-song" described below. Song-spread is given on the territory long before the females arrive, and although it may be given more frequently and extensively in the presence of a female, it appears to be directed mainly toward other males. The presence of a female seems simply to elicit a greater amount of "warning" song.

Female song-spread.—A song-spread display resembling that of the male is commonly given by females (note comparable postures in Figure 1). As in the male, the degree of posturing changes with the intensity of the display. In the "complete" display the bird stands upright, with head raised, tail spread and lowered, with the red-tinged epaulets sometimes erected. The female song, although given with considerable variation, is generally a series of high, shrill and rapid notes, slowing and descending at the end, the last phrase often very sibilant and slurred. It may be rendered "spit-a-chew-chew-chew . . ." or "check-check-a-skew-skew-skew. . ." A more halting and labored call "pee-chee-ta-chee-ta-chee-chee-chee . . ." often leads into the former call and seems to be a more general excitement or alarm call. Song-spread of the female usually is given to other females from prominent positions within her area. Often most of the females present on the marsh may be shrilling or screeching in song-spread to a single female circling overhead. In early May these calls sometimes seem to be the main sound on the marsh, almost eclipsing the songs of the males. Female song-spread has been heard on the study area as early as April 8 (1952), one day after the first females had made their appearance.

Male flight-song.—"Flight-song" is a display given by males which often serves to distinguish territorial birds, although it is given less frequently than song-spread. The full call, always given in flight, is a long, rapid series of notes something like: "tseeee . . . tch-tch-tch-tch . . . chee-chee-chee-chee . . .", (the middle phrase often very nasal in tone, sometimes

FIG. 1 (opposite page) Song-spread display, male and female. All photos taken at height of display, and the figures are arranged to show increasing intensity of display. Note comparable postures of the two sexes.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"tank"). Sometimes only a portion of the call is given, and often the number of notes in each phrase varies, but the call is very distinctive.

What is apparently the same display is mentioned by Allen (1914:90): ". . . a sort of scolding song, which is given in the air, with quivering wings, can easily be resolved into: *check, check, check, t'tsheah.*" The "flight song" described by Beer and Tibbitts (1950:67) may be the same thing: "The victory display or flight song . . . is normally given after successfully chasing a trespassing male from the territory. After the chase has been completed the male slows his wingbeat, spreads his tail and 'parachutes' back to his singing perch. During this display he is in continuous song." I have only occasionally observed this display as an aftermath of an aggressive chase. It is regularly given when leaving or returning to the territory, the return flight often being a long, slow glide.

A rapid call which resembles the middle phrase of the flight-song ("tch-tch-tch . . .") is frequently given during sexual chasing, where it appears to be a scolding or vocal threatening. A similar call was heard on other occasions also suggesting an aggressive motivation. For example, on May 21, 1950, a male gave it repeatedly while chasing a Kingbird (*Tyrannus tyrannus*).

Bill-tilting.—Beer and Tibbitts (1950:67) described a posture assumed by males in mutual threat on their territory boundaries which they called the "bluff" or "stretch display." A closely similar display has been observed in several other icterids. For example, Williams (1952:8) called a probably-related display in the Brewer's Blackbird (*Euphagus cyanocephalus*) the "head-up display." Since the most constant characteristic of this display in the Redwing appears to be the raised beak, I have called it "bill-tilting." Prominent aspects of this pose are the stretched neck with raised beak and compressed body plumage (see Figure 2*a*, *b*). Although the epaulets are exposed in this display, they are never erected. Bill-tilting is most commonly given by adult males on their territory boundaries, each moving up, when suitable perches are being used, as if one bird were attempting to avoid the other without giving ground. On one occasion when two males were tilting to each other in a tree, the uppermost bird moved *down* and even hung down to display to the lower bird as the latter moved up. It is also given by females (Fig. 2*c*), immatures and young. It is mainly an intraspecific display, but both males and females have been observed to give it when confronting other species of birds. Females commonly used it in threat to other females (Fig. 2*d*), occasionally to first-year males, and rarely to adult males. Juveniles used it mainly against first-year males. On several occasions aggressive action was observed immediately following bill-tilting.

Male crouch.—The "crouch" is a tense crouching posture assumed by the

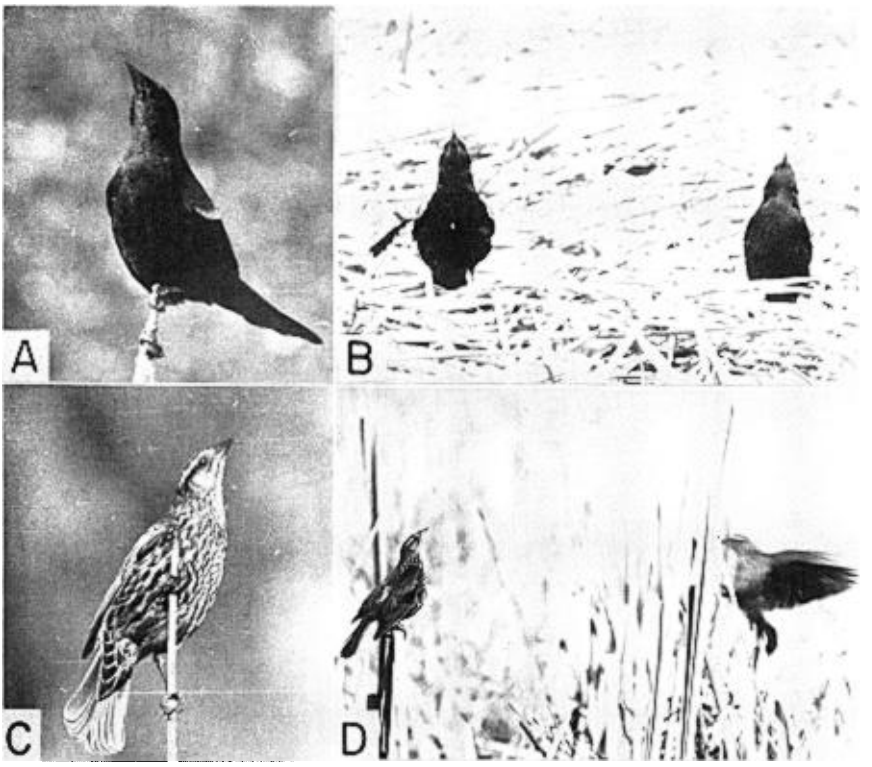


FIG. 2. Bill-tilting display, male and female.

male while perched (see Figure 4*a*). The body is depressed, the head is hunched and held low, the tail is spread and brought downward, and the "shoulders" are held out from the body with the epaulets erected. The wing tips may be crossed over the back or dropped close to the sides. Rarely, the spread tail is momentarily raised. (Males also occasionally held their tails nearly straight up in evident alarm, but nothing comparable to the "elevated tail display" described by Williams (1952:7–8) in the Brewer's Blackbird was seen in the Redwing. Flocks of Redwing males feeding on the ground often keep their tails lifted, a gesture not at all understood.) The crouch posture often is assumed by the male when near one of his mates, usually while facing her, and often preceding further sexual activity. It is also given before new females and before dummy females, but it has not been seen otherwise. Apparently it is an indication of sexual interest.

Female wing-flipping.—During the period of "feeding-the-young" the female frequently raises and flips one or both wings when her mate is

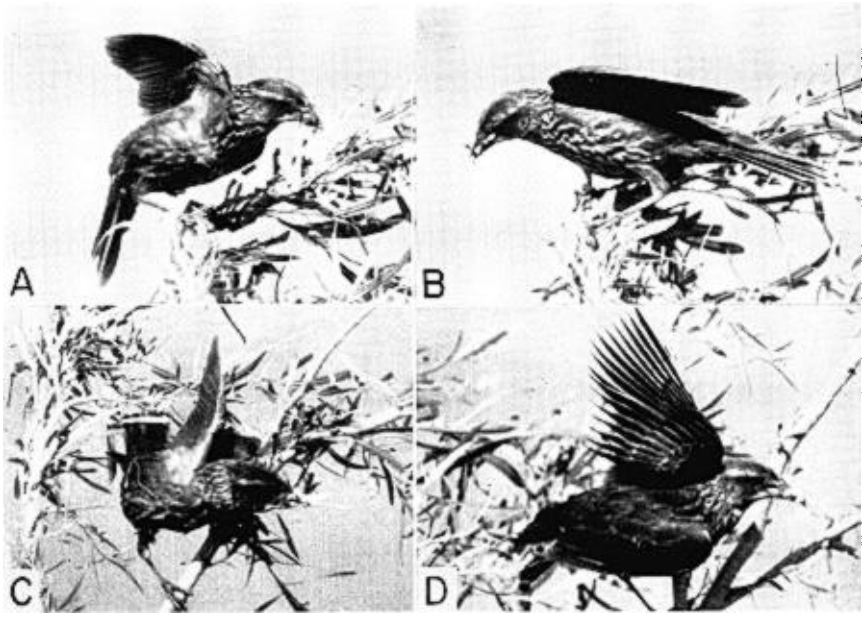


FIG. 3. Female wing-flipping display.

nearby. Such "wing-flipping" involves movement of the whole wing at body level, and, at high intensity, nearly vertically (see Figure 3). In some cases the wing on the side toward the male was held highest. This behavior is apparently not accompanied by any vocalization, but in two cases females held their beaks open. In one instance a female repeatedly bowed "as if to touch her beak to water to drink" and increased her wing-flipping (higher and faster) as her mate approached. Finally the male dived at her aggressively.

Wing-flipping was observed to be given as much as 10 feet from the nest, although it was usually seen at a lesser distance. It was given especially just after a return to the territory with food for the young, and shortly before departure for more food. In one case a female flipped her wings before feeding her young and then kept them raised while actually feeding them. In all of 20 detailed observations of wing-flipping recorded between June 7 and July 16 (1950) the females had young in their nests ranging from one to eleven days old. The mate was always nearby when the female wing-flipped. On a few occasions both male and female have been observed to give a kind of wing-flipping when leading young off the marsh.

One female, whose nest had been transported experimentally into a strange territory, upon being attacked at her nest site by the resident male, raised

a wing on the side away from the male as if in defense. At this time she had eggs in her nest. This is the only instance in which a female with eggs raised a wing to a male. Two days later when the eggs had hatched she raised and flipped both wings to the same male. At the Vilas Park feeding grounds several observations were recorded of females lowering a wing to the ground when being approached aggressively by adult males. The latter usually appear antagonistic to strange females on the feeding grounds. In one case when a female was threatened by an adult male she raised and fluttered her wings at her sides in the manner of a young bird begging for food. The above actions by females appeared to be defensive reactions. According to Nice (1937:57), male Song Sparrows (*Melospiza melodia*) attempting to invade a territory often held one wing straight up in the air and fluttered it as they faced the defending resident male. In one unusual case when a female (which sometimes drive off trespassing males) faced a trespassing male she was ". . . all puffed out and *flipping a wing* . . ." at the male (Nice, 1943:187).

A unique observation was made on an unmarked pair of birds on June 22, 1950, at a lake 30 miles from the study area. A male was seen approaching a female which was perched near a nest. The female began slowly flipping both wings quite high and then, apparently coincident with signs of sexual excitement in the male, she lowered her wings, fluttered them more rapidly and went directly into precopulation display (see Figure 4*h*), quivering her wings and raising her tail slightly. The male soon dropped his excitement postures, but the female maintained hers for a few seconds later.

These observations under normal conditions were supplemented by observations in Saskatchewan in 1955 during an experimental attempt to elicit wing-flipping behavior for photographic coverage (see Figure 3). On July 16 five newly-fledged young were placed in a small cage which was set about 12 feet from the camera. For 1½ hours the female attempted unsuccessfully to feed her young, meanwhile giving extensive wing-flipping before the thoroughly-alarmed male. The female frequently raised both wings, often holding the one of the side toward the male higher, and rapidly reversing wings when she changed position. Much of this sequence was suggestive of the behavior of fledglings begging for food (see Nice, 1950:89). The female continued to show wing-flipping as she searched for food as much as 50 feet from the young and the male, but her wings were held highest when the male was near. Sometimes one wing would be raised over her back and tilted over the opposite side (see Figure 3*c*, *d*). When her wings were held up and shaking, her posture resembled the "elevated wings" of the courting male (Figure 4*c*). In extreme display her wings were raised over her back until they touched and were then directed toward the male, some-

times by tilting or bowing. The male seemed to show some aggression to the female at this point and once raised his wings while pecking toward his displaying mate.

Wing-flipping by the female seems to be an indication of her concern with "feeding-the-young." Just as the male simulates female nest-building behavior during courtship (see Symbolic Nesting) and in moments of anxiety during that stage of their cycle, so the female simulates the behavior of hungry young.

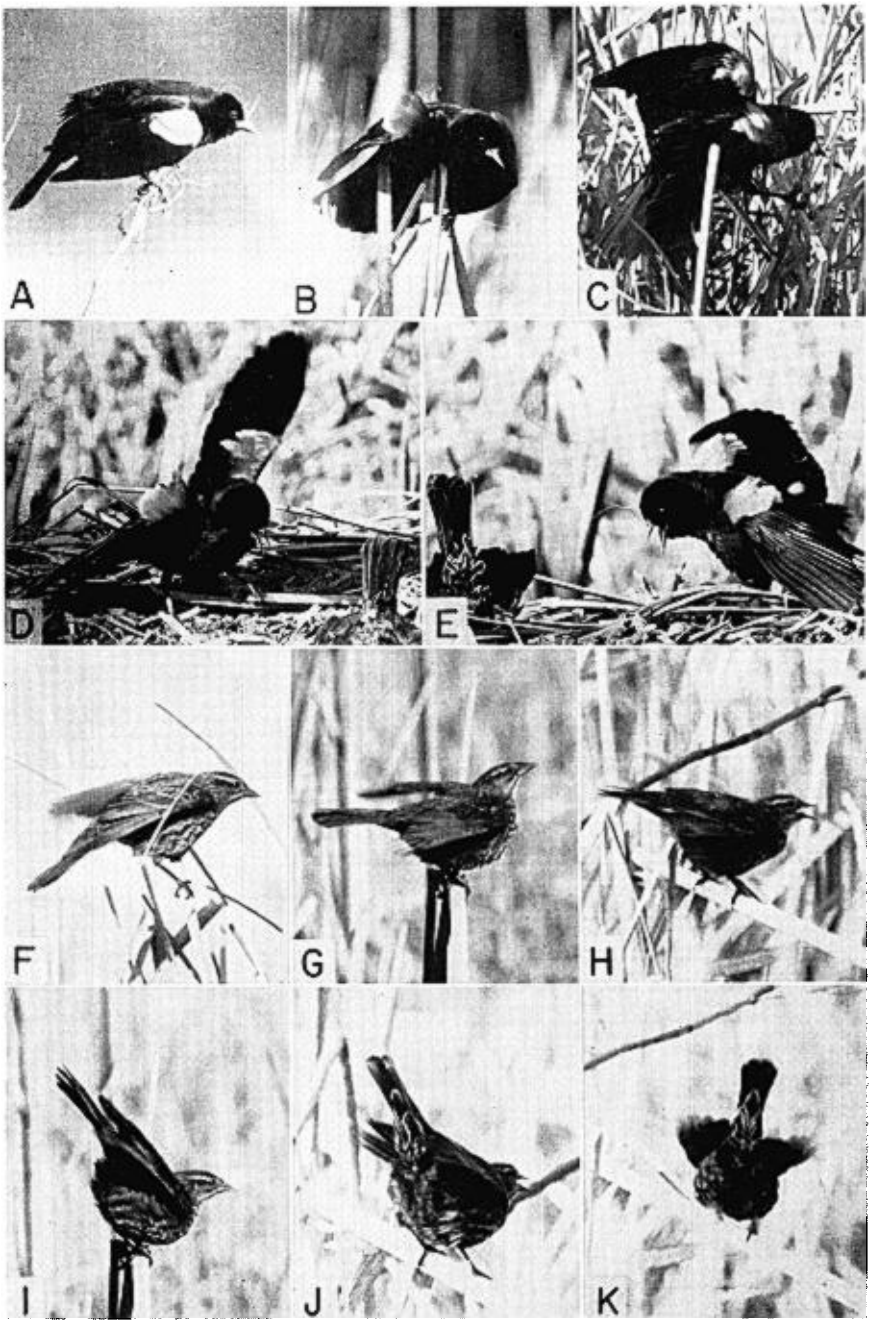
The Pairing Bond

In the Redwing, as in the majority of passerines, the sexes form a bond for the breeding period only. In many species the members of the pair remain together until the young are self-sufficient, but Redwings appear to separate as soon as the female leaves the territory with the young. This must be the case when the male remains on his territory with his other females, but even monogamous pairs apparently separate. Individuals of either sex have been observed caring for young off the territorial grounds, but I have never observed a marked pair together caring for their young off of the male's territory, or at least very far from it. The pairing bond evidently lasts only while the pair is attached to the territory. I made many unsuccessful attempts to observe breeding pairs feeding together outside their territory. Mated pairs only infrequently left the marsh together to feed (the male usually returning first), although males often left in small groups and these birds sometimes fed close together.

In the Redwing the pairing bond does not appear to carry over from season to season as it does in the Brewer's Blackbird (Williams, 1952:9–11). Several of my returning females remated with their former mates but others mated with other males even though their previous mates were present. Nevertheless, females which reassociated with former mates seemed to establish themselves with less effort than did those which acquired new mates.

In Redwings it is well-known that the sexes tend to remain separate throughout the non-breeding season. Males revert to flocking behavior as soon as they quit their territories. My marked males were often seen associating together with other adult males on the Vilas Park feeding grounds in late July and August. In one unusual case a male cared for two of his young until they were 36 days old; during the last nine days of this period he was observed on the feeding grounds in loose association with a flock of males. Females also flock together at this time and move to the uplands with the majority of the young.

Fig. 4. (opposite page) Sexual displays, male and female. Figs. *a-c*: male "courtship"; *d-e*: male precopulation; *f-k*: female precopulation, showing increasing intensity.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Arrival and Establishment of Females

Arriving females are generally fairly quiet and may only give soft "check" or "prit" calls. Single birds or small groups circle in the air over the marsh, or perch nearby and sit quietly or give frequent tail flips until approached by males. Usually the appearance of a new female alerts the males within several hundred feet and various short calls, such as a "check" or soft "ticka-ticka" or shrill "tseee" are given. Some males may sing and fly down to their respective territories; some may stay up on their perches; others may fly up and perch near a female. If a female remains up in a tree, then the males, perhaps several of them, fly up and perch near her, slowly hop along the branches toward her (usually with erect epaulets), and then fly down with song-spread to their territories. Often the females flee at the approach of the males; the latter sometimes fly after them for several hundred feet before returning to their territories. Sometimes these females circle the marsh before flying away and occasionally they suddenly dive into the cattails.

When a female lands in the cattails all the males nearby usually move up to their borders nearest the female and perform a song-spread broadly (Fig. 1*g*, *h*, *i*). The holder of the territory on which the female lands often approaches to within a few feet of her to do this and then displays for several seconds after the cessation of song (Fig. 4*b*). This "after-song" pose is sometimes accompanied by a soft-whimpering "ti-ti-ti-ti-. . ." On some occasions males held their wings spread before they sang. At this time there may be comparatively little song from the holder of the territory. If the female approaches the male he sometimes drops down to the base of the cattails, often down onto the early spring ice, and struts around with wings extended laterally, sometimes rapidly vibrating them, while giving the call mentioned above. Sometimes the extended wings may be partly raised. This display was also given immediately after song-spread with the male perched on the cattails. A similar posturing was observed when males approached a female dummy. In repeated observations of this display before a dummy, the males walked rather stiffly with raised rump feathers and lowered head, occasionally pausing to rest or to give song-spread. This display is similar to part of the male precopulatory display (Fig. 4*d*, *e*). It may be considered an indication of a high level of sexual excitement.

Similar displays were also given on several occasions to other males early in the season before any females had arrived On March 6, 1951, an adult male at least three years old repeatedly held his wings outspread and quivering while giving the "ti-ti- . . ." call. This display was given alternately with full song-spread and erect epaulets to approaching flocks of male Redwings, as well as to approaching individuals, including one first-year

male. From March 12 to 27, 1952, several different males were observed giving this display to other males. It seemed especially to be directed by residents toward new males, which often came in without song and with epaulets more or less concealed. These observations suggest that responses in the male which are normally geared to the female may be set off momentarily by movements or postures in other males which in part resemble or are suggestive of female characteristics. However, this does not imply an outright failure of sex-recognition.

Females sometimes flew in quietly and remained perched near males without making any apparent sound or motion, appearing quite relaxed. Although these females might evoke a display in the male they sometimes flew away quietly afterwards without being chased. Established females occasionally flew into the marsh without arousing any special interest from the males which were apparently able to recognize them as one of their own or a neighbor's mate. In many cases formerly-resident females appeared to arrive at the marsh late in the evening after most activities had ceased. A few which were actually observed dropped right down into the cattails with little hesitation. These females were often found within an hour after sunrise the next morning sitting quietly on a male's territory, behaving like established females, i.e., they stayed on the territory and sang to passing females. Some females showed much "tail flashing," that is, rapid spreading and closing of the rectrices, sometimes accompanied by slight movement of the primaries. (This occurs in both sexes, but is especially prominent in females). Rarely, females visited several territories before finally settling in one, even though they sometimes had remained for several days in one territory. This was regarded as very unusual behavior since ordinarily if a female remained for one day in a male's territory she kept that position. Females which were probably transients (or young?), however, often visited several territories in rapid succession.

Once a female has settled on a male's territory and has become paired she may receive little attention from him, particularly if she remains low in the cattails and quiet. However, her quarrels with other females settling within the territory nearly always bring forth aggressive interference by the male. At times the female follows the male around as he shifts about in territorial defense. She may alight a few feet from him and slowly move toward him, upon which the male usually retreats. The newly-established female may also move toward an adjacent male in the same way for a few days, but in this case she is apt to draw an aggressive response from which she retreats. At other times the male shows an interest in his mate by diving at her, by giving various displays near her, and by sometimes following her off the marsh. Occasionally males followed their females as

they circled high over the territory or marsh. These flights were usually silent and were seldom accompanied by other birds. Generally the male keeps himself between his mate and the neighboring males, meanwhile giving song-spread, especially when they approach his borders. He is always active in driving intruders from her vicinity. Such behavior may be seen throughout the season.

Pair Formation

Pair formation apparently begins (or actually occurs) when a female enters a male's territory. The male appears to assume a proprietary interest in a female which stops in his territory and suitably stimulates him. In several cases when a newly-arriving female which had briefly visited one territory entered another, the owner of the first territory dashed into the next territory to bite or to strike her. These reactions were repeated several times under experimental conditions in which a female dummy was placed in one territory and then moved to another. The first male persistently trespassed in order to strike the dummy in spite of vigorous attacks by the second male. The male thus appears to "claim" the female from the first moment, but the latter's interest appears to be mainly in potential nest-sites. Newly-arrived females sometimes fought hard and long to keep other females from encroaching on their territories.

Williams (1952:9–11) believes that pair formation in the Brewer's Blackbird occurs gradually over a long period right up to nesting. Males and females remain in mixed flocks throughout the non-breeding season, and as the breeding season approaches they begin to show signs of pairing, i.e., they walk about together and the males guard certain females. In Redwings, pairing behavior is *inconstant* at first, gradually becoming more constant as "true" pairs form. Former pairs often reassociate and these show less *inconstancy* than do new pairs. Inconstancy in the Redwing during the period preceding nesting is probably held to a minimum by the territory system. Females attached to one male usually are driven out of adjacent territories by the occupants; moreover, once a female has chosen an area for nesting she shows little inclination to search elsewhere. There is thus little wandering except on first arrival. The concept of gradual pair formation therefore cannot be applied to Redwings. However, some strengthening of the bond undoubtedly occurs through association during the ensuing days of breeding, although it probably never reaches the level of that shown by the Brewer's Blackbird. The stronger pairing bond indicated in the latter species probably results from the longer association of the pair.

Courtship

Symbolic Nesting

"Symbolic nesting" or "symbolic building" are terms used by Nice (1943:

178–179) to describe the manipulation of nesting material by the member of a pair which does not ordinarily help construct the nest, or "unnecessary" handling by the other member (or both, if both build) prior to actual building. Such behavior is characteristic of courtship in many species, from grebes and cormorants to songbirds. According to Nice (*loc. cit.*), although the female Song Sparrow alone builds the actual nest, young males (2 to 3 months old) show nest-*molding* behavior, and adult males sometimes carry nesting material, particularly during the preliminary stage prior to nesting. Both sexes in this species indulge in symbolic nesting, but the male does so more frequently than the female.

Symbolic nesting occurs in both sexes in the Redwing, but it is more pronounced in the male. Since it is also somewhat difficult to differentiate between symbolic nesting and the onset of "real" nesting behavior in the female, I shall refer mainly to the male's activities. His sequence of behavior has been grouped under the terms *symbolic nest-site selection* and *symbolic nest-building* (the former leading right into the latter). This behavior was observed mainly from the arrival of the female on the male's territory until coition and subsequent egg-laying.

Symbolic nest-site selection.—In general, the male "crouches" near the female (see Figure 4*a*), gives song-spread, then flies to a clump of cattails to which he clings, while holding his wings up over his back ("elevated wings," Figure 4*c*). Sometimes he holds this posture for several seconds and may glance back over his shoulder toward the female which often flies down near him. If the female comes, he may leave her to fly back to his perch; but more often he slowly works through the cattails, or *crawls*, still holding his wings partly upright (Fig. 4*c*). Then he stops, *bows* with beak between his feet and bites at the nearby cattail blades or breaks off bits which he manipulates in the manner of a female building a nest. Often the female quietly follows him through the same tortuous path and watches him. This entire sequence, or portions of it, may be repeated many times. Usually this behavior is given to the mate, but on two occasions males gave fragments of it before strange females which flew low across their territories.

The male's flight to the clump is slow and usually appears awkward, the wing-beat being below body level. Sometimes a male will fly from clump to clump continuing this strained flight. A few observations of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) made by me in 1955 convinced me that a pattern of behavior similar to symbolic nest-site selection in the Redwing occurs in that species. Wetmore (1920:403) stated that as the male Yellow-headed Blackbird started toward the female the ". . . wings were brought down with a slow swinging motion and were not closed at all . . ." Ammann (1938) also noticed this kind of flight in

this species and pointed out how noticeable the white wing-patches were at this time. This is apparently the kind of flight described by Howard (1929:9) as expressing sexual excitement. He states: "Two forms of sexual flight are common in bird life; one like the flight of a butterfly, the other like that of a moth. In the former the wings are fully expanded and slowly flapped; in the latter, partially expanded and rapidly vibrated. In both forms the bird travels slowly."

As the Redwing male hits the clump he commonly utters a low, harsh, buzzing "hahh . . ." or "shhh," the "growl," a call often given in threat when harassing other species, immature males, occasionally his mates, and other females (?), but apparently not other adult males. (Females sometimes emit a similar call when driving off other species.) This call is sometimes quite long and is given with open beak, the beak sometimes being held open for a short time afterward. Although generally a low sound, it is quite audible and may be heard from at least 100 feet. Although it may be given at any time during the sequence outlined above, the growl is usually given as the male peers into the cattails, either from the outside of the clump or as he crawls and bows within. On one occasion a male came up out of a clump and faced his mate while giving this call.

While the male clings to the clump his wings may be held completely erect, sometimes even touching over his back; but at other times they may be only slightly elevated and slowly flapped, or held out with only the tips shaking. In one case a male raised and flapped his wings successively higher and faster as his mate approached him in flight. This observation and others suggest that the higher position indicates a greater intensity. In one unique case a male which appeared to be unusually excited during an intense elevated-wing display, uttered a series of short, high-pitched notes which increased in tempo and pitch to the end.

The male's use of the threat call or growl during symbolic nesting recalls the use of similar calls in other species. A "harsh rasping note" was given by a male Mockingbird (*Mimus polyglottos*) when it went into a potential nest-site during symbolic nest-building (Laskey, 1933:31). Tinbergen (1939: 25) stated that during the pre-oestrus period of the female Snow Bunting (*Plectrophenax nivalis*) the male and female frequently go about together inspecting little rocky crevices of the sort in which the female eventually builds her nest. "When entering a hole the male often uttered a sound that to us was indistinguishable from the sound that was heard from a threatening bird. We did our best to detect a possible difference, because we did not expect to hear the same call in such widely different situations, but we must confess we did not succeed."

Occasionally song-spread was given during the sequence. When this

occurred, the sequence appeared to be momentarily interrupted. In several instances males came up out of the cattails to sing and then crawled back and resumed their displays. In one instance a male continued to display when an immature male dived at his female which was watching nearby.

Lack and Emlen (1939:226) state that the male Tricolored Redwing (*Agelaius tricolor*) would often ". . . flutter slowly down into the cattails until out of sight. . . The female sometimes followed, and his behavior presumably influenced her selection of a nest-site and mate." Although male Redwings often went repeatedly to a particular clump to display, I did not observe any case in which a female built her nest in the "selected" clump. In several cases, however, the nest was built within a few yards thereof.

Symbolic nest-building.—Ordinarily symbolic nest-site selection ends with the bowing movement in which occasionally the male bites at the nearby cattail leaves or breaks off bits with which he "plays." However, more elaborate sequences of nest-building have been observed. Two such cases were recorded in May, 1950. In one case a male was courting a female which had been present on the marsh for several days, but which had just come to his territory. This male displayed at the nearly-completed nest of another of his females which was absent at the time. While the new female watched, he went inside the nest and then went through the motions of building, forming it with his chest, lowering his head into it, and picking here and there, meanwhile holding his wings erect. After two minutes the female moved away from him. He went near her and then she followed him back near the nest and again he went through the nest-building behavior, although this time not in the nest. The female moved away from him again and then he once more led her back. Finally he went up to the nest and, while the female watched, he lowered his head into it and then reached outside and appeared to pull in material. This observation is of special interest since in many hours of watching I have never seen the male take part in actual nest-building. A report by Hackett (1913) stating that the male helps construct the nest may possibly have been inspired by an observation of a male engaged in symbolic nest-building.

In a second case a different male, after leading a new female into a clump of cattails, broke off some dead leaves and pulled at a piece of string that had been left there in trapping operations. When the female moved away from him, he went to her, bowed with raised wings and erect epaulets, and then climbed up to an unfinished nest nearby, where he gave the growl call. Then he reached into the nest and picked at the nest material. Later he went through the same behavior with this female in a cattail clump at a different place in his territory.

Such behavior by the male in a species where only the female builds the nest seems remarkable. However, a few cases have been reported in which males of such species apparently constructed complete nests. Dawson (1921: 92) reported that a male Hooded Oriole (*Icterus cucullatus*) ". . . was observed day after day as he constructed a nest on the underside of a palm leaf." And Nuttall (1832:157) tells about a male Baltimore Oriole (*Icterus galbula*) building a nest. Schantz (1937) watched a male Song Sparrow construct a complete nest in which a female later nested. In referring to the latter case, Nice (1943:211) said that the latent nest-building ability, appearing in most male Song Sparrows in the symbolic manipulation of material, developed through practice when this male was mateless for two years.

Symbolic nesting by the male apparently occurs in several other icterids besides the Redwing and the orioles mentioned above, in which the female alone builds the nest. Petersen and Young (1950:467) reported that a courting male Bronzed Grackle (*Quiscalus quiscula*) ". . . repeatedly picked up and moved a bit of paper with his bill, replacing it in a crude nest consisting of a few twigs in a crotch about 25 feet above the ground. He frequently lifted his wings, spread his tail, and '*skreeked*'. The female, perched about a yard away, also held a scrap of paper in her bill, but she remained more quiet than the male." Williams (1952:12) states that in the Brewer's Blackbird "The male of the pair is sometimes the first to hold nesting material in the bill, but he rarely places it at a site." Although symbolic nest-building has not been observed in either of the meadowlarks, a hand-raised male Eastern Meadowlark (*Sturnella magna*) showed nest-molding behavior (Nice, MS, 1950). Mrs. Nice also observed nest-molding behavior in a hand-raised male Redwing at 39 days of age (1950:88). Ammann (1938:116) quoted Wheelock as stating that "she has known the male Yellow-headed Blackbird to make a pretense at nest-building a few feet away from the real cradle . . ." And Ammann (*loc. cit.*) observed males of this species ". . . casually pecking at a few strands of nesting material attached loosely to the reeds near finished nests." Although the parasitic Brown-headed Cowbird (*Molothrus ater*) does not build a nest, Laskey (1950:160) twice saw a courting male Cowbird ". . . toying with a dead leaf or a piece of debris while bowing to a female."

Symbolic nesting in male Redwings as well as in these other species may represent vestiges of functional behavior in a time when the male played an active part in the actual activities of selecting a site and building a nest. Although in nearly all of the Icteridae the nest is built solely by the female, in cowbirds we find at least one exception (Friedmann, 1929). The most primitive species, the Bay-winged Cowbird (*Molothrus badius*), is non-

parasitic but mated pairs locate and fight for the possession of nests of other species of birds which they then occupy. Usually some alterations of the nest are made, and when no nest is readily available they build their own, the *male* generally building more than the female. And in the Shiny Cowbird (*Molothrus bonariensis*), which is parasitic and which normally does no nest building, both male and female have been seen attempting to build. According to Beecher (1950:52) the cowbirds are very close to the original primitive form, the buntings or Emberizinae, from which he believes the blackbird sub-family (Icterinae) has arisen.

Possible functional significance of "symbolic nesting" behavior.—In 1953 I observed that when an incubating female was frightened from her nest by my jerking of the nearby cattails by means of a piece of string, her mate would often come in response to her alarm cries and fly down near her nest. When he withdrew the female would return to her nest. This happened repeatedly. Sometimes when the male was absent or otherwise occupied and did not come to her calls the female would fly about, scolding for several minutes, and would fail to return to the nest until the male arrived. The male's visit nearly always sufficed to quiet the female. Once when a female which was building the basal portion of a nest became greatly alarmed by the click of a concealed camera, her mate flew down near the nest and finally hopped right into it and peered about. These actions of the male somewhat resemble his behavior in symbolic nesting and suggest that the latter may have a "reassuring" effect upon the female.

This interpretation is substantiated by observations of symbolic nesting in "non-courtship" situations. During the egg-laying period the female is irregular in incubation and the male, which sometimes appears restless or agitated when the female is not on the nest, may give symbolic nest-site selection near the nest in what suggests an apparent attempt to induce her to return. On May 28, 1950, in the morning of which a female laid her first egg, her mate was watched from 5:15 to 6:30 p.m., while she was absent. Toward the end of this period the male flew back and forth in his territory and finally flew to the nest and "craned his neck to peer in . . ." From 8:00 to 9:00 a.m., and from 6:00 to 7:00 p.m. the following day, the male went through complete sequences of symbolic nesting (even to the breaking of cattail leaves) near her, but especially near her nest (containing two eggs). He visited the nest in conspicuous display attitude as if in an attempt to lead her into it. On the next day she laid her third and last egg, and again, from 5:00 to 7:25 p.m., her mate repeatedly went through "nest-site selection" behavior. When she finally settled on her nest he flew to the other end of the territory, where he remained perched and quiet. On succeeding days she kept on her nest in more or less constant incubation

and the male no longer showed the "courtship" behavior. In another case (May 22, 1950) a female was kept off her nest by a trap which had been placed directly over it. The male went down near her, suddenly bowed, elevated his wings, and entered a dense clump of cattails where he bowed and manipulated cattail blades while the female watched from nearby.

In many species during the egg-laying period or incubation period the male performs nidocentric displays directed toward its mate. Nice (1943:224–225) offers this explanation: "A bird instinctively responds to certain situations; the situation eggs-in-nest implies mate-on-nest-much-of-the-time; if the second element in the situation is not functioning he is disturbed; if his mate has disappeared he starts to sing (for her or another); if she is around, he tries to get her into the appropriate situation."

Sexual Chasing

Sexual chasing or pursuit of the female by the male during the courtship period has been described for many song-birds (Howard, 1920, 1929; Tinbergen, 1939) and for several non-songbirds (Hochbaum, 1944; Sowls, 1951). It has been noted in the Redwing by Nuttall (1832:171); Audubon (1834:349); Allen (1914:91); Linsdale (1938:141-142); Mayr (1941:53); Smith (1943:190); Mehner (1950); and Beer and Tibbitts (1950:68). Sexual chasing has also been observed in the following icterids: Bobolink, *Dolichonyx oryzivorous*, (Nuttall, 1832:187); Brewer's Blackbird (Williams, 1952:10–11); Brown-headed Cowbird (Friedmann, 1929:158); Yellow-headed Blackbird (Ammann, 1938:102–103); and Wagler's Oropendola, *Zarhynchus wagleri*, (Chapman, 1928:136); but apparently it does not occur in the highly-colonial Tricolored Redwing (Lack and Emlen, 1939:227).

More than 100 sexual chases were recorded in detail in this study. In nearly every case these chases involved birds which had already paired. Howard (1929:70), in discussing sexual chasing (his "sexual flight") stated: "Sexual flight is a certain indication of pairing; I have never known a female desert a male once it had occurred." Sexual chases between pairs of Snow Buntings usually indicated that the birds ". . . had mated and that the female would stay with the male she had chosen." (Tinbergen, 1939:21). Sexual chases in the Brewer's Blackbird are believed to be part of the mechanics of pair formation ". . . since they occur more frequently in pairs forming for the first time and apparently cease when the pair is formed." (Williams, 1952:10–11). Pair formation in this species, however, is considered to be an extended process occurring over a considerable period prior to nesting (see Pair formation).

Sexual chases in the Redwing are usually marked by aggressive pursuit by the male and rapid elusive flight by the female. Females occasionally flew into obstructions and even into the water. Sometimes the female stays

within the male's territory, but often she flies out over neighboring territories. Occasionally these flights take her far from the male's territory, but she usually returns at the close of the chase. Sex chases are often preceded by signs of sexual excitement in the male, and in most cases it is the male who first springs into action, suddenly diving at the quietly-perching female. In some cases, however, it seems to be precipitated by special situations which bring the female into sight of the male. For example, the male seems to be stimulated by the appearance of the female carrying nest material, particularly when she carries it for a greater distance and more openly than is ordinary or necessary. Females in conflict call forth aggression by the male, and this may lead to sexual chasing. Various calls of the female, or simply her arrival on the territory after an absence, may evoke a sudden chase.

The ending of a chase is sometimes as sudden as its beginning, the participants often stopping shortly after they have begun. Usually the male is the first to stop and, as soon as he quits, the female stops fleeing, often landing in sight of the male and usually on his territory. The extreme development of a chase occurs when the male overtakes and hits or catches the female. This may occur in the air or on the ground, either on or off the territory. In seven observed cases the male hit the female or seized her by the rump feathers. In one case a male caught the female in the air and held onto her while both birds fell together some 40 or 50 feet down into the marsh. Hochbaum (1944:42) saw this occur once in Mallards (*Anas platyrhynchos*) and once in Pintails (*Anas acuta*). A male Redwing sometimes held a female by the rump feathers for several seconds while she struggled to escape. On one occasion a male was seen holding a female in this manner for over 30 seconds while she struggled to free herself. In another unusual case a strange male which intruded on a territory to chase another's female, caught her by the rump feathers and then momentarily stood on top of her (female response not apparent). Seizure of the upper tail coverts or the rectrices of the female during sexual chasing has been described for the Reed Bunting, *Emberiza schoeniclus*, (Howard, 1929:7), the Snow Bunting (Tinbergen, 1939:21), and the Canvasback (*Aythya valisineria*) (Hochbaum, *op. cit.*:29).

Biting or seizing of the rump feathers was also seen under experimental conditions. Males which had courted a mounted female in their territories repeatedly flew after it and bit or seized it by the rump feathers when it was placed in a neighboring territory. Noble and Vogt (1935:280) placed a female dummy before a Redwing male on his territory and noted that ". . . he flew back to the female mount and attempted copulation. He then pecked this mount at the base of the tail, both above and below, before

again attempting copulation. . . When the male did not evoke a response on the part of the female mount, he again resumed the cloacal pecking until he knocked the mount to the ground." Only female mounts were so pecked and the authors interpreted such pecking as ". . . apparently a sign of annoyance on the part of the male." (In a similar experiment of my own in June, 1955, a male approached a female dummy which was set up in precopulation attitude in his territory, displayed to it, mounted, showed annoyance and pecked vigorously at the rump and cloaca. "Annoyance" behavior was accompanied by a low "tch-tch-tch . . ." call similar to the call given at the onset of many sex-chases [see below]. In another instance in which a freshly-shot female was propped up with the aid of wires so that the cloaca was clearly visible, the male approached and pecked earnestly at the exposed cloaca. Such behavior may be substitute or outlet behavior for sexual excitement, and there may possibly be some stimulation to the female in these attacks on her cloacal region.

There is some suggestion that female Redwings may threaten strange males which attack them, and in two unusual cases, females apparently momentarily fought with their own mates (May 29, 1950; May 12, 1951). Ammann (1938:102–103), states that when occasionally a male Yellow-headed Blackbird caught a female after a sexual chase the female vigorously resisted the male's attempts to copulate. Tinbergen (1939:21), in describing sexual chasing in Snow Buntings, says that the ". . . female tried to escape and fought with great perseverance" with her mate. And Howard (1929:22) notes that Yellow Buntings (*Emberiza citrinella*), at the conclusion of a sexual chase, may face each other in the air, apparently fighting. Whatever the outcome of a Redwing chase, both members of a pair might be sitting quietly side by side seconds after its end. Similar behavior was observed in Wagler's Oropendola by Chapman (1928:136).

Copulation was never observed as the immediate end of a sex chase in the Redwing. However, on May 25, 1950, a male engaged his female in a sex chase and then, two minutes later, flew up to her again and mounted in apparent copulation, although she showed no signs of sexual readiness beyond sitting still. Eight minutes later, however, she showed extreme sexual readiness (complete precopulatory behavior) and copulation then clearly took place. In his final approach to the female the male's posturing was more extreme than that of his two earlier approaches. Sex chasing may probably be considered an indication of the female's unreadiness. Eventually, however, the female comes into readiness and on such an occasion one might observe copulation closely following a sex chase, as described above.

Song-spread often accompanies chasing, occurring both before and, in

part, even during the rapid flight. A call which resembles the middle phrase of the "flight song" and which has been heard in other situations suggesting a threat function is often given by the male during the chase This call is a high, loud, and nasal "tch-tch-tch . . ." often repeated several times. It may be given before as well as during the chase.

Group sexual chasing.—Often other males from neighboring territories join a chase of the type described above. It then becomes a group chase. Although the basis for a group chase is usually a pair, occasionally a female may become the center of a group chase in the absence of her mate. Even in the confusion of a group chase, it is usually her mate who catches and seizes her. In one case a male returned to strike his female a second time after a neighbor male had intervened to hit her.

Group chases are typically noisy affairs, all males involved tending to give rapid and repeated song and even some spread-display, while on the wing. At this time the typical "oak-a-lee" song is given quite hastily, so that the first part is slurred and the last emphasized. Friedmann (1929:161) describes a similar sexual flight in the Brown-headed Cowbird in which two males were ". . . singing and attempting to display in mid-air . . ." while following a female. It is not clear just what causes other males to join a chase. They always appear interested in each other's chases but do not always join them. The movement of others to join is usually general — when one flies toward a chasing pair, others follow. Group chases in the Reed Bunting appear to be very similar to those described above (Howard, 1929:7). "Owing to some seasonal organic change she is in a condition to stimulate and so to attract. . . as yet she has acquired no experience of boundaries, and straying, passes outside the dominion of her mate . . . she evokes in turn the sexual nature of each neighboring male; and they, on their part, become excited, and their excitement may terminate in the sexual flight." I think that in the Redwing, at least, the group response may often be of a more general nature, perhaps akin to group flocking about a predator. In the course of one group chase, several immature males and females gathered in the vicinity. In some instances groups formed so rapidly that it appeared the males were responding to the chasing pair rather than directly to the female. The "tch-tch-tch" call mentioned above seems to arouse other males. Very often just after a chasing male gives that call, his neighbors fly to join the chase, meanwhile giving the same call. On at least one occasion I have seen males fly to join a chase when the pair was out of their sight behind shrubbery. These birds seemed to respond to the vocalization of the male. In a few cases males evidently were aroused by the calls of others' females. The extended chase, low and over several territories, usually, but not always, brings about group

behavior. Sometimes neighboring males fly into a territory to join a chase which is limited to that territory. The stimulus to chase a female or to join a chase, seems to vary depending on the particular circumstances. It should be noted that the males which join chases are usually themselves in the midst of courtship with their own females, and hence leave their mates to jointly chase another's mate. The behavior of a strange male which catches a female is apparently the same as that of her mate.

Nuttall's statement (1832:171) that during group chase the several males do not show any "jealous feud" with each other seems not entirely true. I think that the great amount of song which occurs during the group chase is an indication of the mutual aggression of the males rather than a direct response to the female. Almost always, at the close of a chase, and often before, the male mate, or owner of the territory on which the group gathers, turns to evict his neighbors. Sometimes the pursuing male even turns away from his female to do this. However, this may not always be the case, especially when the chase ends, as often happens, on a foreign territory or even on a neutral area. What seems more remarkable is that other males which are approaching a chasing pair often turn back in flight when the chase ends.

Group chasing is evidently the kind of chasing that Nuttall (1832), and Audubon (1834) referred to. Audubon's idea that the female Redwing receives the attention of a number of males in group sexual chase and then chooses one of them as her mate (*op. cit.*:349), does not seem in agreement with present observations. Beer and Tibbitts (1950:68) also apparently had such chases in mind when they described a "teasing" flight, involving one female and several males, which purportedly ended in promiscuous copulation. They implied that this was a general occurrence. I have no observation of promiscuity in Redwings, but at the close of one group chase four males in courting postures briefly surrounded a female on the ground and then dispersed.

Stolen matings.—Sometimes in non-promiscuous species, stolen matings occur. Howard (1929:42) says this of the Yellow Bunting: ". . . stolen matings . . . are by no means uncommon where territories adjoin and different females are in different stages of development; and despite the efforts of the owner to prevent it, a male will sometimes succeed — as far as one can tell — in reaching a sexual union." Nice (1943:184–185) says that in the Song Sparrow stolen matings do not occur.

I have no record of a stolen mating in the Redwing, and consider it unlikely, at least on the territorial grounds. Males do cross boundaries to harass another's female, and in one case a strange male even stood on top of the female. However, no copulation was ever observed under such

circumstances. Even at a later time, when the members of the pair are about to copulate, although neighboring males may move up to their near-borders, molestation of the pair is rare or absent. Females generally are recalcitrant to strangers, and their mates are completely so. This is well illustrated by the following observation made off the study area at a place where plowed fields adjoined a small marsh. A resident female flew into the field to feed several hundred feet from the territory, where she was soon joined by a strange adult male. Seconds later she came flying back, giving alarm calls, with the male in close pursuit. When they reached the territory she flung herself into the cattails, and her mate, along with several neighboring males, drove the intruder away.

Period of sexual chasing.—Sexual chasing occurred between members of pairs in varying degree with no particular order of frequency or severity from the first few days of meeting for at least as long as 11 days. In some instances females were with males on their territories for several days before chasing was observed. Sex chases occurred throughout the breeding period, however, owing to late arrivals, remating, and renesting. The period of chasing is possibly correlated with physiological and psychological changes in the female, for once copulation occurred sexual chases were noticeably fewer or absent. Tinbergen (1939:21) stated that in the Snow Bunting ". . . weeks may pass, after the female has taken a mate, before she is willing to copulate . . ." and sex chasing occurred throughout this period. In a few cases a recurrence of chasing was observed in Redwings just prior to second nesting. In one case a violent chase occurred 22 days after a pair had fledged their first young.

The meaning of sexual chasing.—Tinbergen believed that sexual chasing in the Snow Bunting originated from attempts of the male to copulate (1939:30). "When the female did not take notice of the male, that is, when she did not adopt the attitude of readiness, she fled, and a sexual flight originated." The fact that the female flees before the postures or advances of the male is taken as an indication of her sexual unreadiness, since later, upon similar advances, she assumes proper copulatory postures and receives her mate. Howard (1929:11, 40) states that ". . . the behavior of the male is a genuine attempt to complete the sexual act . . . eventually when he flies excitedly towards her and settles beside her, she stays, postures, etc., and copulation results." Nice (1943:174–175) considered "pouncing" in the Song Sparrow analogous to sexual chasing in the above species. (An actual chase does not occur in the Song Sparrow; when the male pounces on the female, the latter usually stands still and at times even fights back.) Nice stated (*loc. cit.*) that ". . . pouncing has no immediate connection with copulation. . . pouncing on the mate may be a technique of the male for

impressing himself upon his mate . . . of making his presence keenly felt!" Although sexual chasing in the Redwing is not connected directly with copulation, it is part of a pattern of actions and reactions which leads to copulation.

Precopulation and Copulation

During precopulatory behavior the female gives a long, rapid series of soft, high notes ("whimpering"). In low intensity the call is slow and these notes seem composed of two sounds: "tse-sit" or "seek-seek," but later the speed of delivery increases and these become: "tsee-tsee-tsee. . . " The rapid series may also gradually become slower and end with double notes. This call may be given alone but ordinarily it is accompanied by rapid spreading and closing of the primaries and, to a lesser extent, the rectrices, while the wings are held close to the body (Fig. 4*f*, *g*, *h*). The whimpering call and wing flutter are usually given while the Redwing is perched, sometimes quite high in a tree but usually on or near the ground. Occasionally the female displays in flight. This display is similar to the female "generalized display" of the Brewer's Blackbird (Williams, 1952:5–7), and, as in that species, is used long before copulation actually begins. It also precedes the high-intensity display (described below). As the intensity of the display increases the female leans forward and lifts her tail and wings, exposing the cloacal region (Fig. 4*i*, *j*, *k*). At high degrees of intensity the female sometimes raises her head slightly while whimpering and fluttering her wings (Fig. 4*g*). Complete readiness for copulation is indicated by both the tail and head being tilted upward sharply with the beak sometimes held open. At this time the body is depressed, sometimes with the breast resting upon the ground or perch. During copulation the female usually rests upon her tarsi with bill and tail still raised. In one observation the female swung her tail to one side and clearly extruded her cloaca just before the male mounted.

The male reacts to the female's precopulatory display by first perching close to her in the "crouch" position (Figure 4*a*). If her display is limited to the whimper and wing flutter he may do nothing more and may pay little attention to her, but on one occasion a male approached while displaying and mounted a female which had been sitting quietly on the ground. When the female goes into full display the male typically drops down to the floor of the marsh, flutters his wingtips while holding them out, either raised or lowered, and gives a soft whimpering cry somewhat similar to the female's, but not as loud and usually not as long. Then, with erected and sometimes violently-shaking epaulets, puffed-out feathers, lowered and spread tail, and lowered head, the male slowly, and often silently, walks stiffly toward the displaying female (see Figure 4 *d*, *e*).

If the birds are in a tree the male sidles along on the branch until he reaches the female. When approaching on the floor of the marsh he sometimes walks for several feet, awkwardly climbing over obstructions. On one occasion a male walked about five feet along the ground toward a displaying female and then, still fluttering his wings, flew up over an intervening cattail clump and landed directly on top of the female which had been out of his sight. Wetmore (1920:403), reported a very similar behavior for the Yellow-headed Blackbird — when approaching their mates, the males ". . . clambered stiffly along, hobbling over masses of bent-over rushes, with heads bent down, tails drooping and back humped. . . "

As the male nears the female he may begin to quiver his wings more and then raise them higher, especially as he mounts. Then he may flap his wings rapidly and sometimes may even hold them almost vertically while on top of the female. He may also do this before mounting her. In a few cases males approached with wings lowered to the ground and mounted the female without raising their wings. The male mounts the female from the rear, slowly moving around her to do this when he approaches from any other direction, since the female usually remains in a fixed position. He remains on top of her for a very short time, perhaps two or three seconds, and then steps off. Usually the male mounts only once but occasionally a male may mount more than once. However, I have never seen a male mount more than three times in quick succession. After dismounting the male usually moves off without any conspicuous display, but occasionally he may continue to move his wings, even though walking away from the female.

During copulation the female is apparently silent and motionless, but afterward she may both call and flutter and sometimes preen. On one occasion the male left the territory shortly after copulation occurred and the female then promptly went into precopulation display again, giving an even louder and more rapid whimpering call than she had previously given.

Wetmore (1920:404), apparently observed precopulatory behavior of the male Redwing when he wrote: "one male . . . often slowly ran along the ground with wings partly spread and half-raised and epaulets showing to their fullest extent, a very pretty display." Tyler (1923:697) wrote: ". . . he faced her with his wings partly spread and, although I was immediately in front of him, I could see practically the whole of his shoulder-patches. . . an actual courting maneuver . . . proved by the immediately subsequent action of the pair."

The precopulatory behavior of both the male and the female Brewer's Blackbird (Williams, 1952:5–6) closely resembles that of the Redwing. Similar behavior has also been noted in the Tricolored Redwing (Lack and

Emlen, 1939:226); the Yellow-headed Blackbird (Ammann, 1938:104); the Snow Bunting (Tinbergen, 1939:29); and many other species.

Length of the "Courtship" Period

The length of the period between pair formation and the laying of the of the first egg averaged 20.7 days for four pairs for which complete data are available. In two pairs which were closely watched, copulation was observed for the first time four days and three days, respectively, before their first eggs were laid. I have no record of copulation after egg-laying commenced, but I have observed females which had eggs in their nests engaged in precopulatory behavior. The earliest record of copulation was April 30 (1949).

Courtship Feeding

In many species of birds the male feeds the female during courtship or during incubation. Usually the male brings food to the female, which begs like a young bird (Lack, 1940). I observed no signs of courtship feeding in the Redwing although it has been reported for the following icterids: Baltimore Oriole (Brackbill, 1941), Yellow-headed Blackbird (Roberts, 1909:374), Rusty Blackbird, *Euphagus carolinus*, (Kennard, 1920: 420), Melodious Blackbird, *Dives dives*, (Kendeigh, 1952:271), and the Brewer's Blackbird (Williams, 1952:13–14).

Distraction Display

I have never observed distraction display (injury feigning) in the Redwing. However, F. V. Hebard states (pers. commun.) that he once saw a male engaged in this behavior. It has been reported in two other icterids, the Eastern Meadowlark (Hebard, MS) and Bobolink (Hebard, MS; Nero, 1955).

Summary

From 1948 through 1953 observations were made of a breeding colony of Red-winged Blackbirds, most of the members of which were individually marked with color-bands, at Madison, Wisconsin.

Adult males arrived between March 6 and April 21. Females arrived between April 8 and May 7. Most of the birds left the breeding marsh by August, but two males were seen within three miles as late as October 23. More than half of all the marked birds returned at least once; a few returned for several successive seasons.

Displays consisted of various movements or positions of the wings, and usually involved exposure and erection of the red wing-coverts. "Song-spread" was the most common of these and was prominent because of the loud vocal accompaniment. Although this is mainly a male display, an

analogous display with a different song was given by females. Males also had a "flight-song" involving a different vocalization. Both sexes indulged in "bill-tilting," a threat display in which the beak is pointed upward to members of the same sex. This was most commonly seen between adjacent males meeting on the borders of their territories. Females often raised and flapped one or both wings when approached by their mates during the period when they were feeding young. The significance of this display was not clear. A tense crouching posture of the male seemed an indication of sexual interest since it appeared to be directed only toward the mate.

Pair-formation began, or actually occurred, when the female entered the male's territory. The pairing bond existed only during the breeding period. The length of the period between pair-formation and the laying of the first egg averaged 20.7 days for four birds for which complete data were available. Single broods were usual, but three cases of double broods (all successful) were recorded. Polygyny was common, but no more than three females ever were observed with one male; two was average.

Male "courtship" behavior consisted mainly in slowly flying away from the female down into the cattails. The male then displayed with wings elevated over his back, crawled through the cattails, bowed, and picked at nesting material. This sequence was termed "symbolic nest-site selection." A related, less common display was called "symbolic nest-building." Sexual chasing, or pursuit of the female by the male, was a common occurrence. Chasing occurred normally between members of a pair during the period between pair-formation and egg-laying. Copulation was never observed at the immediate end of a chase, but chases were seldom observed between members of a pair once copulation had occurred. Neighboring males sometimes joined a chasing pair, forming group chases.

Sexual excitement in females was indicated by a quivering motion of the flight feathers accompanied by a soft whimpering cry. At a higher intensity the tail and bill were raised, the latter sometimes being open. In response to this "precopulation-display" of the female, males assumed a position in which the wings and tail were spread and lowered and then slowly approached the female. Copulation was always of short duration, and usually one mounting seemed to suffice.

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