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AN EXPERIMENTAL STUDY OF TERRITORIAL BEHAVIOR IN BREEDING RED-WINGED BLACKBIRDS

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This paper is concerned with interpretations of the nature and maintenance of territorial and social relationships in the Red-winged Blackbird (*Agelaius phoeniceus*), a semi-colonial polygynous species with highly developed territorial characteristics. It represents one aspect of a broader study of nesting behavior of this species being conducted at the University of Wisconsin.

Studies of territory in birds have been made almost entirely by direct observation of undisturbed birds in nature. A phenomenon so dependent on the complete freedom of the subject as territorial behavior does not lend itself readily to experimental analysis. A few simple experiments, however, were successfully performed by us, and these serve to clarify certain aspects of the territorial relationships of the Red-winged Blackbird. The main technique used was transport of active nests to various points within the territory of a male and across territorial boundaries onto the holdings of neighboring males.

Various ornithologists have experimented with the moving of bird nests from their natural sites. Herrick (1901:1-12, 1935:36) moved nests of various species in order to bring them into better position for observation and photography. This practice has lately become common among bird photographers seeking improved backgrounds and lighting conditions for their subjects. Cross (1949) and others have reported the successful transference of endangered nests over short distances to new places of safety. Nest- and egg-moving have been employed as experimental techniques by several ornithologists to study egg recognition and local orientation (Watson, 1908:224-227; Noble and Lehrmann, 1940; Lashley, 1915:61-75; Johnson, 1941:156-157, etc.). To our knowledge, however, the procedure has never been used for the purpose of analyzing territorial behavior.

The Red-winged Blackbird is an abundant summer resident in Wisconsin nesting in large numbers in open stands of cattail (*Typha*), or in long grass or weeds. Each male defends a small territory on which from one to three females build compact nests suspended from the vertical stalks of the supporting cover. The breeding males actively defend their territories against trespassers of their own sex and are often seen pursuing females. Song and plumage display are well developed and given frequently from established song perches and other conspicuous sites in the territory. The females, dull colored and relatively quiet, take no part in defending the male's territory (Allen, 1914; Linsdale, 1938:140; Mayr, 1941; Beer and Tibbitts, 1950).

This paper describes nest-moving experiments conducted as part of a study of the nesting of thirteen individually marked adult red-wings on five adjacent territories on the 2½-acre East Wingra Marsh of the University of Wisconsin Arboretum at Madison, Wisconsin. Trapping and observing of the birds was started in early April, 1949, and continued until August 16. The nest-moving experiments were carried out during the height of breeding activity from mid-May until mid-July.

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METHODS

All of the birds used in this study (including the young) were marked with colored plastic bands in various combinations plus an aluminum government band. This marking program was a part of the larger study in which nearly the entire red-wing population of the East Wingra Marsh, 53 adults and 90 nestlings, were handled and color-marked. Some of the birds had been trapped and marked on the area in previous years. A 6 × 30 binocular aided general observing and particularly helped to identify individual birds. Color bands were discernible at 50-100 feet in good light and at close range were often visible to the unaided eye.

Most of the observations were made from a small platform built between two trees on the edge of the marsh about 12 feet above the water. In a standing position on this platform the observer could see most of the marsh, and could follow closely the activity of birds in the four territories which served as the focal point of the study (fig. 1). Inevitably, a certain amount of activity took place near the base of the cat-tails where it was screened from view by dense vegetation.

Nests were moved with the clump of cat-tails which supported them. The rhizomes of the clump were sawed through with a key-hole saw and the entire clump lifted and set in an open metal can 18″ × 18″ × 24″ with a screen bottom. The nest with its supporting stalks could then be pulled through the water and, with the aid of a few stones for ballast, set up at any desired point. In order to avoid nest desertion, nests were generally moved in the presence of the female and not more than ten feet at a time.

THE EXPERIMENTAL BIRDS

The locations of territory boundaries as determined by direct observation of threat displays seemed to be definitely fixed within a few feet and did not shift detectably during the seven weeks of the experimental studies. These are shown in figure 1. Territories are labelled to correspond to the letter assigned to the resident male; nests and their female owners are designated by the letter of the male proprietor and a number assigned chronologically as the nests were found; second nests, whether second nestings or re-nestings, are indicated by a subscript figure following the female's designation.

Three females were studied in the experiments described in this paper, while three males and four females provided the bulk of the data on behavior responses. The first experimental female (A1) was subjected to nest-moving experiment 1 between May 31 when the young were half grown and June 4, the day after the young had fledged. On June 23 this female started a second nest and on July 14-15 served as a host to the importation of a foreign nest in experiment 2. Her empty first nest was used in experiment 4.

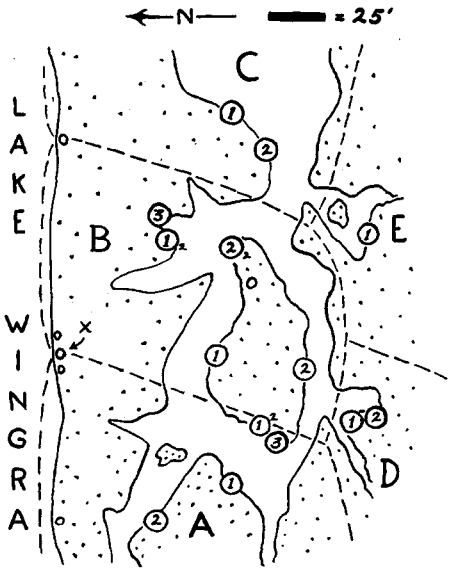
The second experimental female (B1), after playing host to a foreign nest in experiment 1, hatched her first clutch on June 6-7. She disappeared from the marsh with her fledglings on June 15 but was back and started a new nest with the same male on June 28. This second nest served as the subject of experiment 2 between July 11 and July 15. The young hatched and fledged successfully on the invaded territory on July 22.

The third experimental bird (B3) hatched her first clutch on June 4-5. This nest was used in a series of moves which comprised experiment 3. The final move took her into the territory of male A where she successfully fledged her brood on June 14.

All females under observation, whether experimental invaders or hosts, remained with their original mates except one bird (B2) who, after failing in two nesting attempts on territory B, moved to another territory 225 feet distant and successfully raised a brood.

EXPERIMENTS

Details of the four experiments and of the responses observed are outlined below in a condensed version of the field notes. Dates, hours and experimental procedures are italicized. Each item of observation is numbered consecutively for purposes of reference.



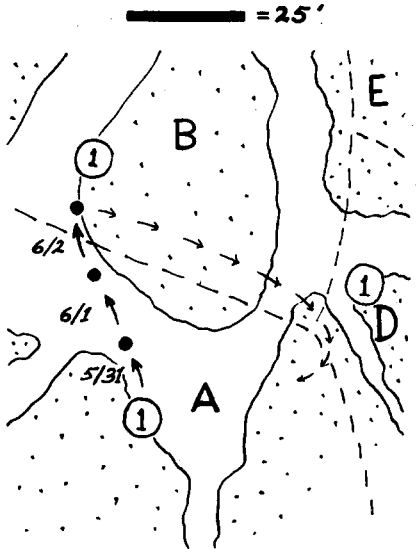


Fig. 1 (left). Location of nests and boundaries of territory B and adjacent areas.
Fig. 2 (right). Experiment I; path of movement of nest A1(1) into territory B and route traversed by female A1 in leading her fledged young back to territory A (small arrows).

Experiment I.—The first nest-move carried nest A1 with four young a few days old over a stretch of open water into territory B. This was done in three steps of about six feet each between May 31 and June 2. Figure 2 plots the steps of this experiment.

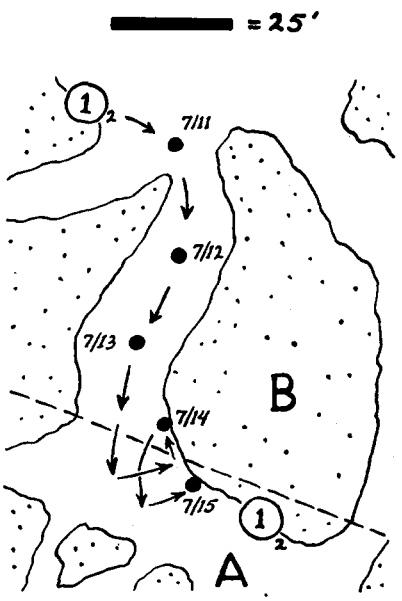
STEP A: *May 31, 4:30 p.m. Nest A1 was moved 6 feet north within the home territory (A).* The female returned promptly and had no trouble finding her nest; no particular excitement was displayed by either male or female.[1]

STEP B: *June 1, 9:00 a.m. The nest was moved 6 feet farther north again within the home territory (A).* The female returned promptly; neither parent was particularly excited.[2]

STEP C: *June 2, 1:30 p.m. The nest was moved 6 feet farther north and just across the boundary into the territory of male B.* Male and female A (the owners of the nest) moved immediately to their territory boundary where they stopped,[3] male B being on his lookout perch.[4] At *1:35* the resident female B1 (nest 6 feet from experimental nest), in her excitement over the disturbance, strayed across the boundary line into territory A where she was promptly repulsed by male A.[5] The excitement continued unabated during the ensuing hour; neither female fed its young although both visited their own nest clumps.[6] At *2:40* the resident and invading females (B1 and A1) fought on territory B; female B won.[7] During the ensuing half hour the invading female (A1) reached her nest 4 times but was driven off each time by the resident female (B1) and twice by the resident male (B).[8] The invading female succeeded in feeding her young for

the first time at 3:00 p.m., the defending birds having relaxed somewhat in their persistence.[9] She fed them irregularly during the rest of the day, under frequent attack by both resident male and female.

FURTHER OBSERVATIONS: *June 4, 10:00 a.m.* On the observer's arrival the young from the transported nest (A1) had fledged and two of them were back in territory A. The other two remained quiet and undisturbed near nest B1.[10] *The two which had reached territory A were experimentally replaced near the nest in territory B for further observations.* The mother bird (A1), rather than cross the open water, led her brood in a roundabout route, skirting the territory boundary and invading a third territory (D) before returning to her home territory (see small arrows in fig. 2).[11] The proprietors of territory B did not interfere, their aggressiveness apparently having subsided.[12] On invading territory D and the vicinity of nest D1, however, both the female and the young were promptly attacked by male D and female D1; and the mother bird was chased back into her home territory.[13] In the excitement male D crossed three times into territory A,[14] where he was promptly driven back by male A who watched closely but never invaded his neighbor's territories.[15] Two of the fledglings hid in territory D and their mother was unable to get to them for several minutes because of the attacks of the resident birds, particularly the male.[16] At *12:00 noon,* the brood, after further harassment, crossed the boundary into their home territory (A) and were no longer attacked.[17] *June 7, 10:00 a.m. A newly fledged young from the nest of the invaded female (B1) was transported, experimentally, back into territory A.* This young bird remained quiet and was not attacked, but the mother was vigorously repulsed by male A when she trespassed over the boundary to feed it.[18]



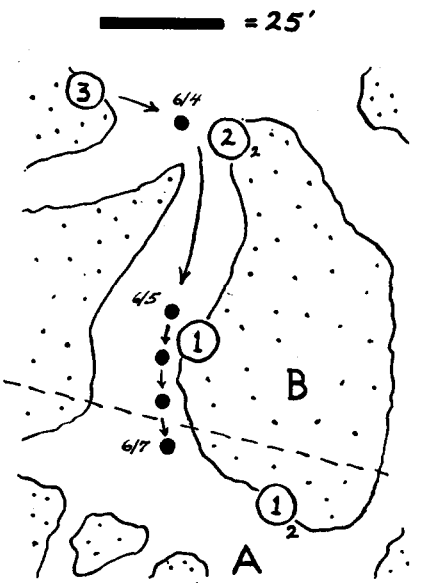


Fig. 3 (left). Experiment II; path of movement of the second nest of female B1 into territory A.
Fig. 4 (right). Experiment III; path of movement of nest B3.

On June 15 male B (the proprietor of territory B) and female B1 led the fledged young of nest B1 off the marsh. Male B returned promptly, followed by one young bird, but female B1 was gone, presumably with the other fledglings, until June 28. On that date, at 6:40 p.m., she was back in territory B, being courted by her old mate. Between courtship displays, this male repeatedly tried and eventually succeeded in leading off

the marsh the one remaining fledgling of nest B1 which he had been feeding during the female's absence.

Concurrently on territory A both parents remained, the female feeding her fledglings until June 27. Courtship, however, was resumed seven days before the last young bird left, and a second nest was started on June 23.

Experiment II.—On July 5 female A1 and female B1 had 4 eggs and 3 eggs, respectively, in their new nests, the locations of which are shown in figure 3. These second nestings provided an opportunity to reverse the situation created by the first nest-moving experiment. Accordingly, on July 11 nest B1(2), containing 3 eggs, was moved southward in the first of a series of steps which carried it over 40 feet into the neighboring territory (A). Figure 3 shows the details of this nest-moving experiment.

STEP A: *July 11, 5:00 p.m. Nest B1(2) was moved 5 feet southwest in the direction of territory A.* The female (B1) accepted the new site within a minute and showed no signs of alarm.[1]

STEP B: *July 12, 11:00 a.m. The nest was moved 10 feet farther toward territory A.* Unlike the preceding moves, this move was made during an absence of the female. On her return she visited first the site where her nest had last been,[2] then the original site and finally, after a few minutes, the new site which she promptly accepted.[3]

STEP C: *July 14, 11:00 a.m. et seq. The nest was carried over the boundary into territory A in a series of short moves.* At *11:00* the nest was moved 5 feet and the female returned promptly.[4] At *11:04* it was moved another 5 feet and the female returned promptly. At *11:07* the nest was moved another 5 feet and over the boundary into territory A; the female hesitated, approached cautiously after two minutes only to retire without reaching her nest.[6] Two minutes later she returned but was driven back by male A.[7] Between *11:10* and *11:17* female B1 flew back and forth in her home territory just over the line from her displaced nest[8] while her mate (male B) called from a nearby tree.[9] Male A, whose territory had been invaded, flew back and forth in his territory in the vicinity of the transported nest but paid no particular attention to the nest itself.[10] By *11:20* the excitement had subsided and female B1 quietly approached her nest and settled on her eggs.[11] At *11:35* she left and mounted a nearby clump of cat-tails where she was immediately attacked and routed by male A.[12]

By *11:45* it was stormy so the nest was moved 5 feet from its exposed site to the protection of bordering cat-tails, still within territory A and about 15 feet from nest A1(2). Observations were discontinued at this time and resumed at *5:10 p.m.*

At *5:15* a call from female B1, incubating on her nest in territory A, brought a prompt approach and then an attack by the resident male, driving her from her nest and back to her own territory.[13] Ten minutes later she attempted to return but was driven back by male A.[14] Again at *5:30* she flew hesitatingly to the nest clump and raised one wing toward male A as he attacked, only to be knocked off and driven back.[15] Four more unsuccessful attempts to reach her nest were made by this female during the next 25 minutes.[16] Finally at *5:55* the nest was brought back across the territory boundary. Unhesitatingly and without interference she entered the nest and settled on it for the night.[17]

At *6:30* a.m. the following morning (July 15), female B1 was flushed and her nest returned to territory A for further observations. Within a few minutes she found her nest and settled on the eggs, apparently unnoticed by the resident male or the neighboring female A1 who were momentarily away.[18] At *6:40* she left the nest for a few minutes and, on returning, was seen by the resident male (A), who flew over her, landed briefly on a perch in territory B in his excitement, left when male B approached,[19] and finally dove down at her in pursuit.[20] He then visited the imported nest, picked up a piece of the nest material in his bill, flew off a few feet with it, manipulated it in his bill and dropped it.[21]

STEP D: *July 15, 8:30 a.m. Nest B1(2) was moved to within 15 feet of nest A1(2) in territory A.* Female B1 soon approached her nest, going very low and quietly and from clump to clump.[22] Female A1 showed no aggressiveness at this time or during the remainder of the day, except for quiet scolding when female B1 happened to fly directly over her.[23] Male A chased female B1 several times during the day but seemed less intolerant of her presence.[24] Once he kept her

away from her nest for 5 minutes, and at 6:50 p.m. he chased her so vigorously that she hit the surface of the water in seeking to escape.[25]

FURTHER OBSERVATIONS: Nest B1(2) was moved no farther. No contact between females A1 and B1 was observed at any time thereafter,[26] although female A1 chased a strange unmarked female from her nest area on July 17.[27] Male A continued to harass female B1 but with diminishing vigor.[28] On July 19 when he attacked her on her nest she raised first one wing and then both wings to him, fluttering them slightly.[29] Both females successfully fledged their broods.

Experiment III.—Following the loss of 4 eggs from unknown causes in her first nest, female B2 re-nested about 10 feet from the nest of female B3 (see fig. 1 for locations). Female B3 (3 eggs) appeared to resent this close approach and on several occasions chased the newcomer who had postured to her in the stiff upright pose commonly assumed by males in defending their territory boundaries. The male, meanwhile, remained on his song perch. Female B2 retained her nest and on June 4 had 4 eggs, while female B3 had 2 eggs and 2 young. By this time aggressive displays had subsided and the two females had apparently accepted each other. Several moves of nest B3 were then initiated to test the tolerance of neighboring harem-mates and to shed further light on boundary recognition (see fig. 4).

STEP A: *June 4, 5:00 p.m. Nest B3 was moved 6 feet south, to within 4 feet of nest B2(2).* Neither female appeared much concerned; both soon settled on their nests.[1]

STEP B: *June 5, 8:20 a.m. Nest B3 was moved about 15 feet west, to within 2 feet of the empty nest B1(1).* (Female B1 still had young in the nest area.) This nest move was made during the absence of female B3. At *8:30* female B3 returned with food in her bill and began to look for her nest near nest B2(2) where she had last seen it.[2] She visited nest B2(2) and apparently dropped her food in with the 4 eggs in that nest.[3] A moment later she left hurriedly as the owner (female B2) attacked.[4] Male B promptly dove to a nearby perch and the disturbance stopped.[5]

After a few minutes female B3 found her nest and flew to its edge.[6] A moment later female B1 also landed on the same clump.[7] There was no quarrel between them; and both females soon flew off quietly to look for food for their young.[8]

STEP C: *June 7, 9:30 a.m. Nest B3 was then moved 18 feet west to the channel of open water which marked the boundary between territories A and B.* This move was made in three steps with intervals of sufficient duration to permit the female to feed her young at each successive station. She quickly accepted the final site in the channel between the two territories.[9] At one point she alighted on the cat-tails in territory A, the resident male being absent at the moment.[10] When male A returned and saw her on the cat-tails in his territory he immediately dove at her and chased her back to territory B.[11] From then on she approached her nest clump more cautiously, coming in low and slowly.[12] While she fed her young, male A generally watched and scolded from the cat-tails in his territory.[13] Male B offered his mate no assistance, but scolded from a tree nearby.[14] Male A chased female B3 on many occasions during the ensuing week, particularly when she entered the cat-tails in his territory,[15] but female B3 successfully raised her brood at this site.

Experiment IV.—A few simple experiments were conducted one afternoon to test the effect of an empty nest suddenly placed close to the nest site of a breeding female.

STEP A: *June 4, about 2:00 p.m., an empty nest was moved to within two feet of the recently vacated nest. (B1).* (Female B1 still had fledged young in the vicinity of her nest.) Female B1 scolded a little but did not seem to direct any attention toward the nest.

STEP B: *About 20 minutes later the empty nest was moved to within 1 foot of nest B2(2) which held 3 eggs.* Female B2 was curious but went to her own nest in a few minutes without apparent alarm.

STEP C: *About 15 minutes later the empty nest was moved to within 1 foot of nest B3 which held 2 eggs and 2 young.* Female B3 quietly inspected the empty nest without any apparent alarm and was on her own nest in 3 minutes.

DISCUSSION

The behavior precipitated by these few experimental transplantings of nests gave rather consistent results which are summarized below and discussed in the light of pertinent published observations on the Red-wing and other species. The roman numerals in the parentheses refer to the experiments as outlined above, and the arabic numbers which follow refer to the observations noted under each experiment by superscript numbers.

Preciseness of territorial boundaries.—The boundaries of male territories were sharply defined and, especially in areas where nest-moving accentuated border defense, could generally be drawn within a foot or two. These boundaries occasionally followed the edges of cat-tail clumps, but often showed no special relation to recognizable features of vegetation or terrain. They were quite stable after nesting had started, no record of a shift having been recorded during the seven weeks of the experimental period. General observations of sharp territorial boundaries have been noted for the Red-wing by Mayr (1941:77) and by Beer and Tibbitts (1950:66).

The degree of preciseness demonstrated by the Red-winged Blackbird is apparently rare among birds except for certain "lek" species such as Manakins and Grouse in which the males defend small and narrowly circumscribed courtship territories in the lek and take no further part in breeding activities. Sharply defined territories comparable to those of the Red-wing have been described for two other species which pair for the breeding season: the Bishop-bird (*Euplectes hordeacea*) (Lack, 1935:822) and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) (Linsdale, 1938:129, Fautin, 1940:79-80). Both of these species also resemble the Red-wing in being colonial and polygynous in their nesting. The highly colonial and polygynous Tri-colored Red-wing (*Agelaius tricolor*), however, has a less precise type of territory boundary (Lack and Emlen, 1939:225).

Territorial exclusiveness.—Males defended their well-defined territory borders against invasion by other males (I–15, II–19, and other instances), alien females (I–3, 4, 8, 11, 18, II–7, 12, 13, 14, 15, 16, 20, 25, III–11, 15 and other instances) and alien fledged young (I–13, 17 and other instances).

Exclusion of other males is usual among territorial birds, but aggressive repulsion of females and young by territorial males is unusual in sexually dimorphic species. The sex of the invader seems to determine the response in most species, but as Lack (1939: 187), Tinbergen (1939:55) and others have noted, the mating status of the invader may alter this response. In the Red-wing, a territorial male differentiates sharply between females of his own harem, and those of his neighbor's. Similar behavior toward trespassing females is exhibited by *Euplectes hordeacea* (Lack, *op. cit.*) and *Xanthocephalus xanthocephalus* (Fautin, *op. cit.*), both, like the Red-wing, being colonial nesters with polygynous mating habits.

Alien fledglings were generally driven from the territory, but in four cases (I–10, 12, 16, 18) they were tolerated. The reaction toward fledglings was thus less definite and regular than toward alien females and may represent merely an irregular extension of the proprietory aggressiveness displayed toward females. Lack (*op. cit.*) noted a similar aggressiveness toward fledgling Bishop-birds, but Fautin (*op. cit.*) did not find it in the Yellow-head.

Resident fledglings reared on the territory were tolerated and fed for as much as two weeks by the resident male who differentiated sharply between his own and strange fledglings. We have no record of a Red-wing feeding alien young on its territory.

Recognition of territorial rights.—Combined with this stiff defense of territorial

boundaries the male Red-wings under study showed a definite recognition and respect for the boundaries of neighboring territories. Trespassing simply did not occur under ordinary circumstances when the owners were present. During the absence of a bird, neighboring males occasionally ventured onto his domain for brief periods but retired promptly with his reappearance. In no case did males attempt to follow nests transported out of their own territories in experiments I, II and III; nor did they offer any assistance when their mates were persistently attempting to penetrate the defense of a neighboring male to reach their nests or young (II–9, III–14). Often a male would approach to the very boundary of his domain only to stop and face his neighbor, a foot or two away, in threatening posture.

This rigid observance of the territorial rights of neighboring males may be a natural concomitant of the active and precise type of territorial defense described above. Such well defined territorial organization may tend to reduce the incidence of fighting and lead to social stabilization in some such manner as a definite social organization has been found to reduce social conflict in flocks of domestic hens (Guhl and Allee, 1944: 347). Certainly the Red-wing, in its crowded nesting colonies, fights much less than does the American Robin in which territorial behavior is vague and territory recognition undeveloped (H. F. Young, in press).

Females generally restricted their movements on the marsh to a fraction of their mate's territory in the nest vicinity. They apparently showed no cognizance of the male's territorial boundaries except where their own limited sphere of activity confronted a neighboring male's holdings (I–16, II–15, III–12). This cognizance, furthermore, was detected only when a nest was experimentally moved toward a boundary so as to precipitate clashes. It thus appeared to be a specifically learned response to the local situation rather than a general recognition of the mate's possessions as such.

Tinbergen (1936:7, 1939:64), in reviewing the evidence for several species, postulates that females do not recognize the mate's territory boundaries as such. In species where females as well as males are actively repulsed at the territorial boundaries, however, a learned recognition of neighboring claims might be expected among females.

When drawn into strange territory by experimental nest-transplanting, females assumed a subordinate attitude toward the residents (I–16, II–15, III–12) and were invariably defeated in clashes with the residents whether these were males (I–3, 4, 8, 11, 18, II–7, 12, 15, 25, III–11) or females (I–3, 7, 8, II–27). On two occasions a female, on being attacked at her transported nest by a male, stiffly raised one or both wings (II–15, 29).

Tolerance of invasion.—Males in the present study were never tolerated on a territorial holding. Flights over established territories cannot be regarded as true invasions since the birds did not pause long enough to permit an attack. Temporary invasions by neighboring males during the absence of a territory holder have been observed by us and by others, but again carry no implications of tolerance. Such invaders leave promptly with the return of the owner.

The repulsion of females other than the mates appears to be nearly or quite as definite and inflexible as the repulsion of males. The barriers to female invasion were, however, broken or lowered in a number of cases in the present study as a result of the pressures created by nest moving. An examination of the circumstances of these incidents permits an analysis of the male's intolerance of alien females. Invasions by females can be conveniently classified into three categories: (1) inadvertent invasions by females not recognizing, or temporarily ignoring, a territorial boundary; (2) quiet trans-

gressions of the territorial line unnoticed by the male; and (3) successful penetration of the male's defense through persistence.

The majority of instances of boundary penetration by females (I–5, 8, 18, II–7, 12, 15) occurred during periods of general excitement and can be classed as inadvertent. A smaller number occurred during the absence of the defending male and were promptly terminated by his return (II–18, III–10). Such instances are of interest from the point of view of boundary recognition but carry no implications of tolerance by the territory defender.

While territorial exclusion by the male Red-wing was characteristically extended to all strangers, regardless of sex or age, several instances were noted in which the barriers of exclusion were partially or temporarily lowered to quiet and inconspicuous females (II–11, 12, 22, III–12) and fledglings (I–10, 12, 16, 18). Aggressive behavior toward the latter appeared and disappeared abruptly according to whether they were moving about or resting quietly. Linsdale (1938) noted that Red-wings, in an established colony in Nevada, tolerated young Yellow-heads (p. 142) or a nesting pair of Yellow-heads (p. 143) as long as they were perched, but pursued them whenever they became active. These observations are in line with the conclusions of Lack (1939:51-53), Tinbergen 1939:55) and others, that aggressiveness by a territorial bird is evoked particularly by displays of aggressiveness or defiance by visitors, and that the recognition and acceptance of females as mates in certain monomorphic species depends on the absence of such displays.

The third category of territorial invasion, penetration of the male's defense through persistence occurred when (a) the defending male relaxed his vigilance, perhaps from fatigue, after a period of boundary activity (I–9, II–11), or (b) the male, after a period of several days or weeks, partially lowered the barriers of exclusion for certain individuals who repeatedly trespassed to reach their transported nests (I–12, II–24, 28, III–15). The situations which led to the first type (a) were the result of experimental manipulations and probably would not often arise in nature. Excitement precipitated by other disturbances at a breeding site typically follows a similar pattern of climax and regression, so the declining aggressiveness of territorial males was not altogether unexpected. Territorial penetration of the second type (b) occurred without exception when nests were left on the invaded territory and suggests the gradual acceptance by the male of those females who became familiar to him through repeated contact.

Individual recognition has been detected in territorial defense by several authors, notably by Lack (1935:823) who observed that in two sympatrically breeding and closely similar species of Bishop-bird, females of the opposite species were tolerated if, but only if, they were local residents familiar to the territory holder.

The lowering of the boundary barrier for certain females in the Red-wing contrasts with the response displayed toward contesting males where a complete shift of the line of separation appears to be the only adjustment possible. The difference suggests that the territorial aggressiveness displayed toward females may differ in motivation from that displayed toward males. At least it would be dangerous to assume that the exclusion of females in this species is a quantitative extension of the competitive exclusiveness characteristically displayed toward males. The special reception of these females may be a secondary response to specific individuals after they have become familiar individually to the male through repeated contact; it may even be akin to the acceptance of unattached females as mates earlier in the season.

The role of the nest.—Although the nest is the focus of defensive behavior of the

male Red-wing against human invaders, it apparently has little significance to the male in his repulsion of other Red-wings from the territory.

Males circling over a human invader characteristically accentuated their excitement in the immediate vicinity of nests. In the absence of such disturbance, however, they showed little interest in the nest itself and rarely visited it. Excitement over the importation of alien nests was directed at the female owner who attempted to follow, and never, with one possible exception, at the nest itself. In this single exception (II–21) the unusual behavior seemed quite undirected and casual.

The nest-moving experiments described in this paper indicate that the nest with its natural support carries more significance to the female Red-wing than the nest vicinity *per se*. Females readily accepted the experimental displacement of their nests and followed them as they were moved in steps of ten or even fifteen feet for distances of up to forty feet within the male's territory (I–1, 2, II–1, 3, 4, 5, III–9).

Nests moved to a new site in the presence of the owner were quickly discovered and promptly accepted; those moved in her absence were found after delays of a few minutes and immediately accepted (II–3, III–2, 6). Apparently the excitement created by the disturbance did not blind the bird to what had been done, and the single observation was efficiently utilized by the bird in making the adjustment to the new site. The long learning period displayed by Watson's terns (1908:225) was to all appearances summarily bypassed.

Female Red-wings also attempted to follow their nests as they were experimentally moved across territory boundaries (I–4, 6, 8, 9, II–6, 8, 14, 16). No parallel situations are known to us in the literature, but the well-known persistence of many female birds in defending their nests against enemies makes the response not unexpected. Nice (1943:188) records an incident where a female Song Sparrow vigorously fought and finally gained local dominance over a neighboring male on whose territory her nest was located. Tinbergen (1939:40) cites a similar case in the Snow Bunting where the objective was a fledged young.

Response to nest encroachment.—As already noted the object of male aggressiveness appears to be the territory with its sharply defined boundaries while the focus of female aggressiveness is the nest and its vicinity.

Aggressive defense of the nest area by females was directed toward female harem mates, alien females (from other harems) and alien fledglings. Fighting among harem mates was infrequent except early in the cycle. In one case (introduction to III), the relationship was mildly aggressive during the nest-building and egg-laying stages but quite peaceful thereafter. Experimental approximation of nests showed that females advanced in the cycle tolerated the close approach of harem mates (III–1, 7, 8) but repulsed an actual invasion of the nest proper (III–4).

The relationship of females to female intruders from other territories was strongly aggressive in most cases (I–3, 7, 8, 13, II–27). The repulsion of such intruders was often effected in company with the male, and it is possible that the strong aggressiveness displayed was influenced by his presence. Only one member of the harem, the one whose nest vicinity was violated, participated in the disputes which followed nest importations, but no clear boundaries to the defended zone were detected. Owners of transported nests were, as noted above, dominated by the residents and even when at the nest or with the young showed no defensive resistance (I–8, 13).

Fledglings from neighboring nests were apparently accepted by nesting females without alarm, but young birds from more distant nests on other territories were, in the one observed instance, driven away when they were active or noisy (I–13).

As with the males, female intolerance appeared to subside with time and repeated contact. This was seen in the reduction of intraharem conflict as the nesting season advanced (III–introduction, 1, 4, 7, 8). It is also suggested by the unexpected acceptance of the imported female in experiment II by the resident female who had become acquainted with her through extended contact one month earlier in experiment I (II–23, 26).

SUMMARY

Experimental moving of nests within and across the boundaries of male territories in a small nesting colony of Red-winged Blackbirds substantiated direct observations of the authors and of other workers on Red-wing behavior. They also served to demonstrate and clarify various characteristics of territorial behavior not previously described. The observations may be summarized as follows:

1. Males recognized sharp and stable territorial boundaries which could be defined within a few feet.

2. Males vigorously defended their territories against the intrusion of alien males, females or fledglings except when the latter were quiet. They tolerated the introduction of alien nests.

3. Males did not extend their aggressiveness beyond their territory boundaries even in the defense of their mates or nests in neighboring territories.

4. Females freely followed their nests as they were moved experimentally through the territory of the mate, but assumed a subordinate attitude and followed with difficulty when their nests were transported across territory boundaries.

5. Females took no part in the defense of the male territory but opposed the encroachment of alien females on their nest vicinities.

6. Males eventually accepted alien females which persistently invaded their territories to reach transported nests.

7. Harem mates (female residents of the same male territory) tolerated each other at close quarters after nesting had gotten under way but repulsed actual visits to the nest. Members of neighboring harems tolerated each other after they became acquainted.

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