

A BEHAVIOR STUDY OF THE RED-WINGED BLACKBIRD¹

II. TERRITORIALITY

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THE first portion of this study (Nero, 1956) dealt with the behavior of the "Redwing" (*Agelaius phoeniceus*), particularly as related to mating and nesting activities. The present paper describes the formation, maintenance, size and structure of the male territory; female territorial behavior; and behavior of first-year (one-year-old) males, as observed in the vicinity of Madison, Wisconsin.

TERRITORIAL BEHAVIOR OF ADULT MALES

Male intolerance.—The territory of the male Redwing is a clearly circumscribed portion of the breeding grounds from which he repels Redwing males, females other than his mates and, at times, even fledgling Redwings. Territorial boundaries are well-defined and fixed throughout a season, the boundaries often being maintained within a few feet or less (Nero and Emlen, 1951). Resident males responded to strange males by first giving song-spread, then bill-tilting, and then flying to attack (but usually displacing the intruder without actual contact). (For description of bill-tilting and song-spread see Nero, 1956:9–12.) These three responses probably represent increasingly greater threat displays. The direct, fast flight toward an opponent also seemed to have an intimidatory effect. Further aggression was shown by a sudden "crash-landing" with which males often displaced intruders. This was often accompanied by the threatening "growl-call" (Nero, 1956:22) and an antagonistic open-beak display.

A resident male's aggressive intolerance extends to a wide variety of birds on or near his territory. Between 1948 and 1951 I recorded incidents wherein 20 species (of 13 families) were threatened or attacked; often the individuals were merely chased. Redwing males were persistently aggressive toward Bronzed Grackles (*Quiscalus quiscula*) and Long-billed Marsh Wrens (*Telmatodytes palustris*), which were nesting on the marsh, but they seemed only temporarily interested in evicting other species. In spite of the impressive array of evicted species, three male Cardinals (*Richmondia cardinalis*) were once observed singing on the marsh unmolested. The nesting male's aggression toward the human species is well known, but deliberate encounters with Sparrow Hawks (*Falco sparverius*) are probably rare. On two occasions I watched Redwing males triumph in fights in mid-air (beak to beak) with this species. Hawks of other species elicited a different reaction. Redwing

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alarm whistles (high and shrill) passed from marsh to marsh when hawks were first sighted. Nearly all Redwings on the marsh sat quietly on their perches with concealed epaulets when hawks were soaring overhead or when they were perched nearby. It seemed that different species drew different responses, but this was not clearly documented. Redwings responded to accipitrine hawks, which were actually hunting on or near the marsh, by suddenly diving down into the cattails to hide or by flying in a group high above them. The admirable boldness of the male was sometimes exhibited by his mate, particularly in conflicts with the Marsh Wrens and Bronzed Grackles. On one occasion when a sheep approached an upland Redwing nest the female owner attacked first, landing on the sheep's forehead; she was later joined by the male which landed on the rather unperturbed sheep's nose. Under this onslaught the mammal withdrew. The largest and heaviest "opponent" which I ever saw evicted from a territory was a large plow-horse which had come to the edge of a lake to drink. A male Redwing clung to the horse's rump and pecked determinedly as he plunged toward higher ground. Nevertheless, the tiny Warbling Vireo (*Vireo gilvus*) has often driven my Redwing males from the vicinity of its nest in the trees bordering the marsh. Determination and "moral right" often decide the "victor," but so does opportunity: Redwings frequently chased other species after the latter had taken flight!

Size and Shape of the Male Territory.—Individual territories were roughly square, rectangular, circular, or highly irregular. Some variability was presumably due to response to the pattern of the marsh vegetation. It seems probable that the presence of a high song-perch also had some influence on territory shape. Nearly every territory included a tree and in several instances birds which were located centrally on the marsh had territories with long extensions out to the trees along the edge. Mayr (1941:78) found a similar situation in New Jersey. I found that whenever a tree branch was artificially set up in the cattails in a territory it was quickly utilized as a perch by the resident male. Territory size appeared to be strongly affected by the pressure of other males. New residents, especially those which moved into a well-populated area, often had very small territories. These might be suddenly increased through disappearance of an adjacent male, or gradually, as a result of persistent aggression.

The average size of 17 territories of well-established males during incubation and fledgling stages of breeding was 3,550 square feet (roughly corresponding to a 60-foot square or approximately one-twelfth of an acre). The minimum size was 1,330 square feet (about 1/32 acre), the maximum size, 6,280 square feet (about 1/7 acre). Linford (1935) found much larger territories in Utah: average, 31,603 sq. ft.; minimum, 17,292 sq. ft.;

maximum, 45,903 sq. ft. Twelve territories of the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) measured by Fautin (1940:78) averaged 1,294 sq. ft. (range, 760 to 2,275).

Territory size generally varied inversely with population density. In 1947, 14 males shared the eastern one-third of the marsh (Beer and Tibbitts, 1950:75); in 1953 the same area was divided among only seven males, nearly all parts being completely utilized and defended. The territory of one persistently-returning male showed a constant increase in size from 1949 to 1953 (1,326 sq. ft., 3,125, 4,400, 4,450, 5,350). Similar data for other individuals were not obtained. Although territory size increased, the number of females per male remained about the same, the female population having decreased during this period. In 1947 Beer and Tibbitts (*loc. cit.*) found 91 nests with eggs in the marsh. From 1950 to 1952 I found, respectively, 50, 38, and 35 nests with eggs. In 1953 two cooperating students, Messrs. Roy Gromme and Norbert DeByle, found only 27 nests. These figures are probably complete in all cases, as the coverage was thorough.

Incipient Territorial Behavior in Transients.—From March 20 through 28, 1952, I observed many adult males (unmarked) apparently occupying definite areas in the tops of the high trees across the road on the south side of the marsh. These birds behaved in many respects like typical territorial birds, showing complete song-spread and fighting. This behavior was possibly associated with the heavy migration which occurred at this time (in 1952 the marked residents arrived between March 17 and March 30), and suggests the appearance of the territorial urge in migrants.

These "temporary residents" often flew considerable distances to drive off other males and then returned to their original positions. Often two or more of them perched close together without showing any intolerance, but they gave song-spread to newcomers and also drove the latter birds away. Some of the temporary residents flew away after a short time, but others remained for several hours. Some of them showed an interest in the marsh as well as the tree-top area, but the many new males which frequented the tree tops seemed to offer more attraction. The temporary residents gave some displays which are usually given to females and in some cases appeared to contest with their associates for the right to display or to chase newcomers. For example, on March 26, when a new male approached the tree-tops without song and with his epaulets covered, one of the temporary residents gave song and displayed to him, and at once another temporary resident flew to them and chased the displaying bird. The new arrival meanwhile flew after the chaser and seized his tail momentarily while in flight. Perhaps aggression was aroused by the sight of display, so that while associates at rest ignored each other the display by one to a new bird provoked an attack. Similar

behavior was not observed on the marsh, owing perhaps to the stable conditions of the territorial system.

A few birds appeared to be more persistent and later showed an interest in the nearby marsh by at times swooping down over it with song, although returning to their tree positions. Some of these may have been true residents, but lack of marking made this impossible to ascertain. Some resident males on the marsh, particularly those with territories adjacent to the trees, also tended to utilize the tree-tops, apparently in response to the temporary residents and migrants.

REESTABLISHMENT OF TERRITORIES BY RETURNING RESIDENTS

Beer and Tibbitts (1950) have shown that there is a strong tendency for former residents to return each year to the same breeding grounds and also to hold the same general area as a territory. On the first day of their arrival former residents usually appear wary and are easily flushed, but in a short time, even by the second day, they become less wary. At this time it is sometimes possible to determine their territorial inclinations by simply forcing them to move several times, their movements often being within a limited area (often corresponding to their territory of the previous year). In the early spring they may be found on their territories in the early morning and late afternoon, giving song-spread, particularly from one or two special song-perches, within or on the edge of their territory, and constantly flying out onto the cattails to sing or to confront neighbors (Fig. 1).

Some early arrivals show a tendency to occupy a territory larger than that which they had held in the previous year, retracting as other birds move in and take up territories. Residents which had previously held small territories usually attempted to enlarge their holdings and often succeeded. Most birds, however, remain within the approximate boundaries of former territories. Former residents generally seem more casual about territory establishment than do new birds; that is, they appear to be more tolerant of trespassers.

Respect for boundaries is apparent even in the temporary absence of the owner, although trespass is then more frequent. Residents occasionally trespassed for short times on other territories in order to drive off strange adults or first-year males, to engage in sexual chases with females, and to harass predators. When a female which has been on a territory with a male flies to another territory, the first male may dash across the border to strike the female and then hastily return, sometimes even before the neighbor has a chance to drive him back. On at least one occasion when this happened, the female flew back to the original male's territory. These conditions

provided one of the few occasions upon which males persistently crossed territory boundaries. Similar reactions were elicited when a female dummy was moved from one territory to another, the trespassing "husband" continually returning to the dummy even though severely attacked by the second male. A trespassing male usually shows signs of recognition of the territorial rights of neighbors. This was clearly seen in the above experiments. Each time the "claiming" male invaded a neighbor's territory to "visit" the dummy, his epaulets were concealed and he never gave song-spread, but each time he returned to his own territory he immediately gave song-spread with fully-exposed epaulets. Similar behavior was observed when a male trespassed in order to feed on a piece of bread placed a few feet beyond his boundary.

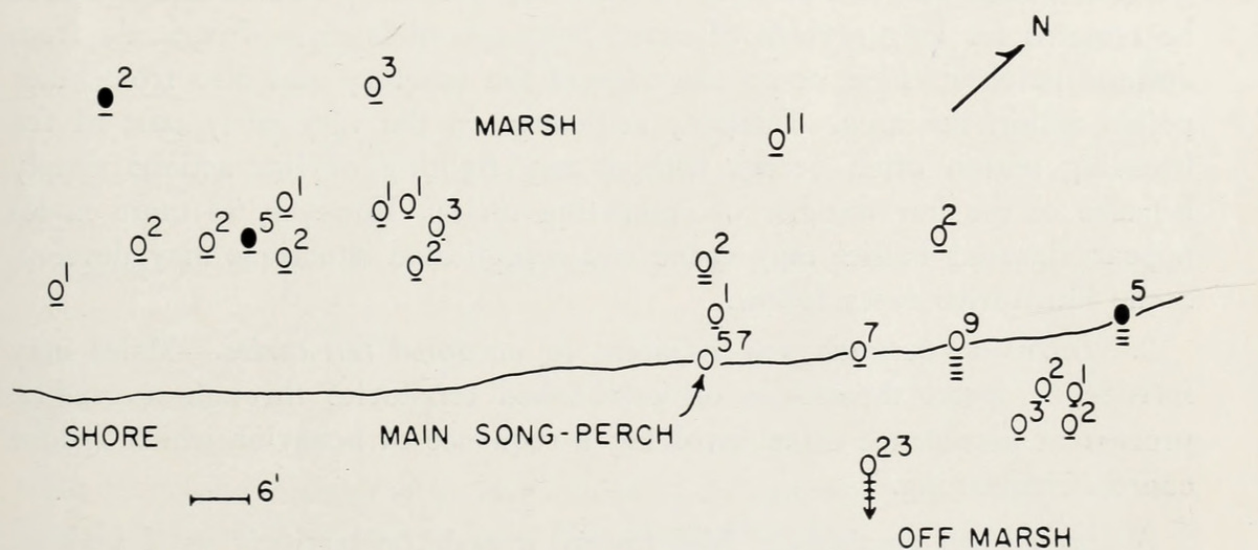


FIG. 1. Activities of one adult male, 7:00 a.m. to 9:30 a.m., March 30, 1948, showing time spent on the main song-perch and excursions into the territory. Circles indicate areas visited by the male; lines beneath the circles, number of visits; figures, total number of minutes at the site; dots, encounters with other males. Most, but not all, visits were made directly from the song-perch.

In cases where adjacent males returned a second year, territory lines often closely followed those of the previous year. Males whose territories do not adjoin may not have developed the tolerance or mutual respect, possibly developed in the previous year, which characterizes settled neighbors. For example, on April 5, 1953, it was first noticed that a resident male had disappeared and that his neighbor to the north had moved onto his territory and was being attacked furiously by the neighboring male to the south with which he had previously had no contact.

Nevertheless, well-established males continue to meet on their boundaries throughout the breeding season. There seemed to be a tendency for adjacent males to face each other at rather definite places along the border of their

territories, especially where shrubs or trees provided higher perches. Ordinarily these contacts are confined to mutual bill-tilting, but occasionally quite severe fights occur. Meetings of this sort arise primarily from movements or behavior of the resident females which bring about sexual responses in neighboring males. A male seldom interferes when his wandering mate is aggressively repulsed by the neighboring male, but when the latter approaches the border with obvious sexual response he is immediately met by the "guarding" owner.

ESTABLISHMENT OF TERRITORIES BY NEW BIRDS

1. *Territorial establishment on unoccupied areas (early in season).*—In general, a male selects a location to which he constantly returns and in which he remains for long periods of time. Song-spread is given frequently from definite perches within or on the edge of the territory and also from other points within the area. Territory settlement in the very early part of the breeding season often occurs without any fighting or interactions simply because of the low number of competing males. However, as more males appear vigorous battles may ensue and complicated situations may develop. Some illustrative cases follow.

2. *Intrusion between and adjacent to occupied territories.*—Males may intrude or insert themselves on established territories through a gradual process of persistence often involving a sequence of behavior which I have called "challenging."

A new arrival persistently flies toward a male on territory as if inviting chase and when this occurs retreats or dodges ("testing the male"). He flies low over the territory with slowly-moving down-held wings, alternately gliding and flapping ("testing the territory"). Sometimes as he glides over the territory he suddenly looks back over his shoulder toward the resident ("head toss";=bill-tilting?). When the resident flies toward him the intruder retreats, or dodges and circles about the territory, now fast, now slow—sometimes gliding, as the resident moves. In this fashion the intruder leads the resident, which keeps above him, higher and higher, ever circling, sometimes until they are hundreds of feet in the air and sometimes far from the territory ("soaring flight"). Often during the flight the intruder swoops and pecks at the resident, and vice versa. The resident attempts to keep above the other, alternately gliding and flying "in step" with him, until one or the other breaks off. Then the intruder either flies elsewhere or back to the territory, and the flight begins again.

New males may challenge or make sorties at several males on the territorial grounds, as if attempting to find a suitable opponent. For example, on March 26, 1952, at 5:30 p.m., a new male was seen challenging several

residents, one after the other, all surrounding a central area on which the new bird was focusing its attention. Soaring with the first male lasted well over four minutes and took the two up in the air about 200 feet. The newcomer persistently returned to the center of the marsh and glided over the cattails with head up, thus invoking immediate chase by the nearest male, which he would then lead up in soaring flight. He did not land on the cattails, but glided over them and then headed for an individual. Although as many as three birds chased him at one time, only one of the three followed him up into the air.

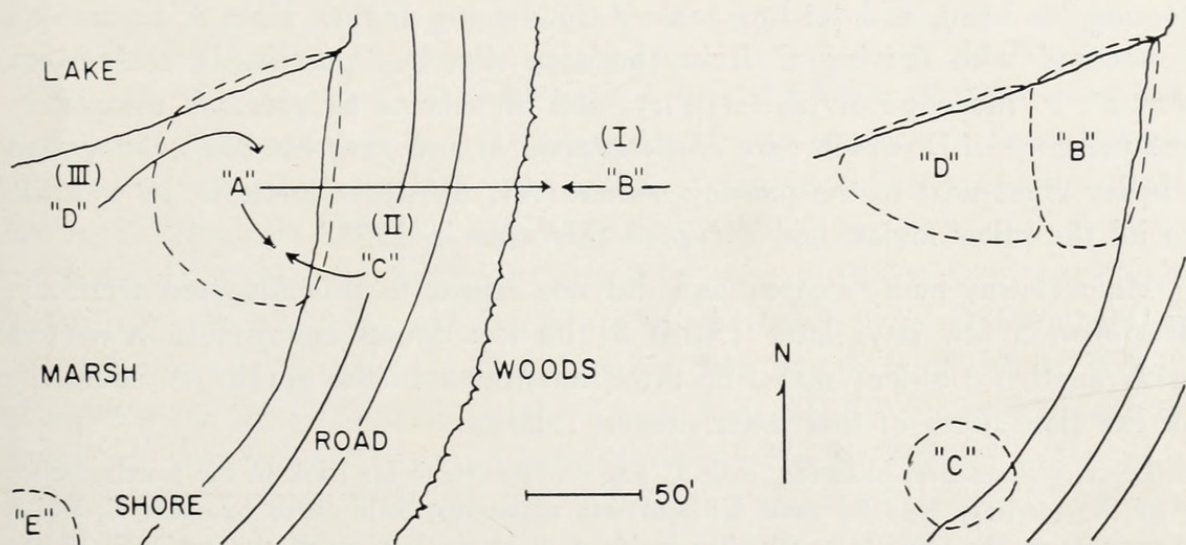


FIG. 2. Spatial relations of 5 males, March 20 to April 24, 1952. (Left map) (I). Male A held male B far back in woods from March 20 to April 21. (II). On March 30 male C arrived and challenged male A. (III). Male D quietly took over a portion of the territory during the period when male A was fighting male C. Male A was trapped on April 21 and disappeared following his release; D and B shared the area subsequently (right map). Male C, beaten by male A, finally established a territory farther south (April 24).

In other instances a new male "selected" a particular male to challenge. From March 20 to April 21, 1952, the owner of a territory, A, forced a challenging male, B, to remain at bay, some 400 to 500 feet back in the woods away from the territory (Fig. 2). Whenever male B made the least approach toward the marsh, the resident immediately flew toward him and repulsed him. The bird thus held back in the woods (male B), repulsed all other males from his vicinity just as if he were on territory, even though the area he occupied was unsuitable as a nesting area. When male A became concerned, eight days later, in chasing and fighting with a second, more aggressive rival, C, male B moved up to the edge of the territory. Each time when the owner returned, however, he quickly withdrew. The situation remained as above up to April 21, with male B pushed even farther back

into the woods away from A's territory. On April 21, male A entered a trap, and male B moved in and occupied a portion of his territory opposite another rival, D. The latter male had easily intruded during the period that A was concerned with male C which was driven away. The trapped owner was released but disappeared (his remains were later found in the marsh, possibly killed by a mink) and B held his portion of the territory through the remainder of the breeding season.

Male C had performed beautifully as a challenging male, engaging in all the stages of the pattern, gliding over the territory, swooping at male A, tossing his head, and leading male A in soaring flight. Male A became so concerned with driving C from the area that he "permitted" male B to venture to the edge of his territory, and he seemed to overlook completely the presence of D, which very easily slipped in and gave extreme song-spread display right next to the panting owner (A). However, male D, in contrast to all the other males, had occupied this area in 1951.

Male C was badly beaten and did not return to this disputed territory. However, a few days later (April 3) he was found engaged in a contest with another resident male, E, three territories to the south. A summary of the field notes of this latter contest follows:

- 5:00 p.m. When first observed, male C was on "territory" far back in the woods (south of the territory held by male E) and was apparently held there by male E, which sang from the cattails to another resident at times but spent the majority of his time on the trees across the road, apparently watching male C.
- 5:10 After 10 minutes C began flying toward E, making short flights directly at him, but always swerving aside at the last moment. E usually at once darted at him and each time male C returned to his distant perch.
- 5:20 After 10 more minutes he began flying toward E and then swerving past him toward the territory; but he always retreated whenever E moved toward him. But C appeared to have gained some ground, he was closer to the edge of the woods, and he seemed more confident. A short while later C began striking at E, but always dodging and withdrawing before E's attacks, and then leading E up into the air in soaring flight. They circled higher and higher, making short darts at each other and then came down again, and C returned to his distant perch, probably to rest.
- 5:35 Fifteen minutes later E sailed down to his cattails and C at once flew straight in to join him, sailing over the cattails in a similar fashion. But at the first sign of attack by E, male C retreated. E then showed his ownership, almost seemed to flaunt it, by parachuting onto the territory with song-spread display, and as soon as he did this C flew right in to him and, as he passed by, E pecked at him and drove him back.
- 5:40 This again led to the soaring flight. No matter how high they flew E always kept above C and often tried to peck him. But C maneuvered from side to side and nicely eluded his attacks.
- 5:45 Male C sailed first over the territory and of course E at once drove him off. C constantly provoked a fight, but always retreated.

Finally C sailed into the territory, hovered over the cattails with raised head and then returned to the woods. Again and again he did this, never landing, while male E watched closely but did not chase. Then E soared down to his territory and landed while C cruised over him and then retreated to the woods.

5:55 E chased C numerous times as the latter flew past him. Male C kept coming closer, but he was always on the dodge. He "tested" the territory by hovering over it, but he did not land, nor did he stay to fight. He did this again and again, ever more frequently, and finally he *went down low* over the cattails when E chased him. He went through this behavior dozens of times more and, as he sailed and hovered over the territory with raised head, looking back over his shoulder, there was no mistaking his challenge.

6:30 At 6:30 male C succeeded in *landing* on the edge of the territory, if only for short moments, and then he finally *remained* there facing male E with song-spread.

The next day (April 4) at 8:30 a.m., C was still back in the woods, but he flew straight and low to his "beach-head" on the edge of the territory (on the border of E territory and another) where he sat low and under cover and singing. Male E, meanwhile, sat high above him, also singing.

Observations were discontinued until 5:45 p.m. At this time it was found that E had entered a trap and C was now uncontested owner of the territory—and he plainly showed it. The situation was left thus (April 4, 1952). (However, on April 23, 1952, male C was dominated by a new male and forced off his territory to an adjacent position—see 3b, below.)

(On April 22, 1955, I observed a challenging male flying over a territory and being driven alternately by three residents. The challenger never sang once during 1½ hours of observation although the three residents sang with extreme display. When I placed a mounted male in the "wanted" territory the resident bird paid no apparent attention, but the challenging male dived down at the dummy several times when crossing over the territory. It seemed as though the challenging male "resented" the dummy more than did the resident.)

3. *Displacement of established residents.*—Sometimes males intrude on established territories in the presence of the owners by simply appearing on the area and persisting in the face of attacks by the residents. Occasionally, however, they show immediate dominance over the resident. Three cases illustrating this phenomenon under various conditions are recounted below.

a. *An old resident is dominated.*—A remarkable case of an intrusion occurred in May, 1953, when a male which had been a resident since 1948 was completely dominated and forced off his territory by an unmarked adult male. This case was first noticed on the morning of May 5, when the resident male, which had arrived on March 21, was seen resting on the edge of his territory while the new male sang from the resident's favored perch. Throughout the period of observation the intruder drove the owner with

fierce attack whenever the latter attempted to move into the territory. The resident was seen returning to the area in the late afternoon, but he was immediately driven across two territories by the new male. The resident was not in sight the morning of the next day, but at 5:30 p.m. he was found on his territory, giving extreme song-spread near a trap which held an unbanded male, presumably the intruder. The trapped male was removed from the marsh and the resident held the area for that season and the next as well.

b. *A new resident is dominated.*—In another case, shortly after the arrival of a female on a territory, and probably before the pairing bond was fixed between the male and the female, a second male appeared and rather quickly dominated the resident, forcing him off of his territory onto adjacent holdings. Neither bird had held the area in the previous year. This case is described in detail below:

Male C (second-year adult) held a new territory from April 4 to April 21, 1952. No observations were made on April 22. In the afternoon of the following day a marked female and an unbanded adult male (distinguished by a broken feather in one wing) were present on his territory. The resident bird was also present and was clearly being dominated by the new bird. The full story follows:

5:00 p.m. Male C is being threatened by an intruder which actually attacks him on his own territory! He follows the resident about, crouches above him, flies above him as he flies, drives him constantly—in short, completely dominates him, so that the resident is forced to sing while in flight over his own territory much like an intruder. The new male attacks him constantly, wherever he goes. There is a battle in the cattails, and then another; the resident always losing. The resident drives at the female, then flies at the new male which at once drives him lower down into the cattails.

5:15 p.m. The old resident makes another pass at the new bird which now seems more excited and gives an even fuller display. There is a great deal of bill-tilting between them, especially by the resident when the new bird approaches him. They both tilt and walk up on the song-perch. It is clear that the resident does not display as much as the new bird. The owner displays most when in flight gliding over his territory. The new male often gets above him and displays down to him.

5:30 p.m. The action continues as above with the new male constantly driving the old resident which has moved farther east onto the next territory (whose owner remains aloof) from which area he makes futile attempts to return to his territory. Finally they engage in a furious fight which takes them up into the air; again and again they engage in aerial combat.

April 24, 4:00 p.m. The old resident and the new bird are apparently still engaged in the duel, but to a lesser extent, for the resident seems to have moved to the east of his territory, the male in that area having withdrawn for him.

5:15 p.m. The old resident now sings from a new perch 70 feet to the east. He remains there for 20 minutes even though the new bird which now holds his territory is temporarily absent.

He subsequently held a territory in the new area and the male which evicted him held the original territory.

c. A male loses a portion of his territory including a female and her nest.—

In this case a newly-arrived male seized a portion of a resident's territory in which a female had already built a nest. The female stayed with her nest and later mated with the new male for a second brood. Since this is a unique occurrence it is presented below in some detail.

Male F arrived on March 28, 1952, and quickly occupied essentially the same area he held as a territory in 1951. On April 16, female F appeared on his territory. She had been a resident in 1951 on an adjacent territory with another male. This female associated with male F for at least the next 18 days (until May 3). No observations were made on May 4 or 5, but on May 6 a newly-arrived male, G, in adult plumage for the first time (second-year male), was observed holding a portion of F's territory which included female F's completed nest. Male G was also courting a new female (G). On this day male F still showed an attachment to female F, but also a respect for the new male. On May 20 and 28 male F still showed an interest in and a tolerance of female F, but on June 3 when she was feeding fledged young he seemed antagonistic toward her.

Since it was not clear whether male and female F were entirely separated a simple experiment was performed on June 4 which showed this to be the case. Two caged young of female F's brood were placed in territory F and for half an hour male F kept female F from feeding her young. Female F later nested again but with male G. She was seen with him on the marsh on July 10.

* * *

Male Song Sparrows (*Melospiza melodia*) show a "challenging" behavior when attempting to intrude on established territories (Nice, 1937:57-58). The intruder puffs up like a ball, often holds one wing up and fluttering, and sings rather constantly and rapidly, if often incompletely. The defender sits silent and hunched in menacing attitude, following every move of the newcomer, which sings in flight from one bush he wants to claim to another. "Soon the owner begins to chase the intruder, but the latter, if determined, always returns to the spot he wants to claim." The two finally fight and either the intruder is routed or the resident retreats. In a later work Nice (1943:155) considers the "puff-sing-wave" behavior indicative of the "... threat of a bird at a temporary disadvantage." Even returning residents adopted a subservient attitude to new occupants of their old territories, but the old birds soon reversed their roles and regained their territories. An old Song Sparrow was never observed to be defeated. This was not, as noted, always true in the Redwing.

In the Robin Redbreast (*Erithacus rubecula*), Lack (1946:41-43) observed eight encounters in which a new male attempted to dispossess another of its territory. In six cases a kind of "challenging" behavior, a "... formal procedure, of alternate loud singing and chasing, was continued all over the territory." In two of these encounters "... the dispute ended with the newcomer leaving the territory." But in three the owner left, and the newcomer took possession. Fighting in these cases was minimal. The newcomer in one case "... did not attempt to strike the previous owner; it seemed just to wear it down by persistence."

The male Reed-Bunting (*Emberiza schoeniclus*), according to Howard (1929:5-6), sometimes invades established territories by persistently clinging and returning to a corner of one. He is "... so insistent in maintaining his position that he breaks down all opposition: and in the course of a few days his rival yields, retires to the opposite corner of his ground and there makes for himself a new headquarters."

Brown and Davies (1949:77) report the following for the Reed-Warbler (*Acrocephalus scirpaceus*): "Sometimes the encroaching male may take over the entire territory and perhaps the nest and hen of the original owner. Sometimes the encroaching male may be completely repulsed, in which case he will almost certainly try to elbow himself in on some other territory in which he may find weaker opposition. Between these two extremes there will be all gradations from the cock which manages to establish himself in a small territory, to a cock which almost but not quite swamps the territory of the bird into which he is encroaching." The same may be said for the Redwing.

COMPETITION FOR TERRITORY SITES

Response of extra males to a vacancy.—Territory-seeking males appear commonly on the breeding area throughout the season. The absence of a resident bird through death or even his enclosure in a trap immediately sets the stage for the appearance of new birds. The pressure of males and the complications which may develop under these circumstances may be shown by the following case.

On May 4, 1950, (at 1:45 p.m.) two resident males, H and I, were found in traps which had been set early in the morning in their respective territories. Two new males, H1 and I1, were in possession of their territories. Male I was held but male H was released. At once H returned to his territory and drove the new male, H1, away from his territory. Male H1 then moved over to I territory and quickly dominated the second new male, I1, forcing him to leave the marsh at 2:23 p.m. although the latter (a banded bird) continued to visit the territory.

At 2:35 the resident male I was released. He flew to his territory, bathed quietly and then left, with his territory in the possession of H1. The latter had flown down near him but had not attacked. At 4:40 a third new male, I2, appeared and quickly dominated H1. I1 then returned and remained. These three birds quarreled over the area until 6:15 p.m., when observations were discontinued. At 5:00 a.m. the following morning, male I was found in complete control of his territory and the three temporary occupants had disappeared. I arrived in time to see him drive an unmarked adult from his territory.

Responses of established males to new neighbors.—Established males usually contend more with new neighbors than they do with their old associates, but the amount of interaction varies with circumstances and individuals. Most new males are quickly integrated into the territorial system, especially if they observe the established boundaries. However, aggressive efforts to expand their holdings create active disputes. Contacts occur generally only when territories are contiguous, and former residents usually remain within their territories. Occasionally, however, former residents, subjected to persistent aggression, move beyond their boundaries to retaliate.

In one unusual case in 1950 a new male was persecuted by several residents at the same time. Although this male showed the typical behavior of a territorial male and used full displays and complete song at all times, he was driven by six different males until he eventually relinquished his claim. Although he backed off in the face of aggression he always responded with full displays. One wonders why this bird elicited constant and vigorous aggression from all the adjacent males (some even left their territories to attack him) when those birds which preceded and also followed him on the same area did not.

BEHAVIOR OF FIRST-YEAR (ONE-YEAR-OLD) MALES

Territorial.—It is well known that male Redwings do not generally breed until their second year, by which time they have also attained the adult plumage. A few observers have noted occasional first-year males holding territories (Beer and Tibbitts, 1950:65) and even breeding (Wright and Wright, 1944:58), but there are no published observations on the behavior of first-year males on territory and their relationship with adults. Wright and Wright (*loc. cit.*), have shown that males come into active spermatogenesis in their first year, although their testes reach a maximum in May, three weeks later than those of the adults, and are not as large as in the adult. Beer and Tibbitts (*loc. cit.*) stated that first-year males “. . . do not usually have the drive to establish a territory for themselves.” They observed first-year males establishing temporary territories three times. In

each instance the territory was only maintained for two to three weeks, from about the middle of April until the first week in May.

There is no record of a first-year male breeding on the study area, but in 1950 I found one about $\frac{1}{4}$ mile away in the company of a female near an empty nest. Both birds were evidently feeding fledged young, although these young were not found. The pair was seen in the same place from June 19 to June 24, (both having been trapped and color-banded). Neither bird was seen after the latter date. The neighboring, resident adult males had shown the usual recognition of male territory boundaries. On June 23 I observed several adult males driving other first-year males away from the territory of the absent, resident first-year male. An adult male circling above me in alarm quickly left when the resident first-year male appeared and took his place. In most cases the few first-year males I observed holding territory on the study area quickly retreated before adult threats, but they also appeared to be treated by the adults with a certain amount of deference (or indifference?) at times. In two cases first-year males behaved as active territorial birds for several days and then suddenly withdrew although apparently undefeated. The song-spread of these birds seemed as complete as that of the adults, although they lacked the brighter plumage. The urge to hold a territory simply seemed to wane after a few days.

The temerity of first-year males is also evident from the numerous occasions upon which they have been seen to pursue and hit adult males while in flight, even seizing them by the tail. On one occasion when this occurred the adult turned about and the two birds fought with beaks and toes while in mid-air. A moment later the chase was resumed with the first-year bird again driving or following the adult (April 30, 1950). Most encounters of this sort seemed to be with non-territorial adults. It is evident that first-year males sometimes may behave like adults and show bold and aggressive territorial inclinations. Under such conditions they appear to be treated in much the same manner as intruding adult males, except that the resident adults show a much greater tolerance toward them. First-year males only rarely succeed in breeding; ordinarily they seem to lack persistence in maintaining a territory.

BEHAVIOR OF FIRST-YEAR MALES TOWARD FEMALES AND YOUNG

Throughout the breeding season first-year males often attempted to approach resident females on the breeding marsh. In nearly all instances the females gave a loud, rapid, and shrill "pee-see-hee-hee-hee . . ." sometimes accompanied by fluttering wing tips (that is, rapid opening and closing of the primaries). The resident adult males usually responded by flying up at once and driving off the first-year males. Females were never receptive

to first-year males and often escaped their advances by diving into the cattails when the latter came close. The females showed a special reaction to first-year males, often bill-tilting and sometimes giving song-spread, responses which they have seldom, if ever, been seen to give to adult males. In one case a first-year male approached a female whose mate was momentarily involved with another male and thereby drew more responses than are ordinarily seen. Each time he flew toward her the female fluttered her wing tips and screeched; finally she bill-tilted and pecked at him as he sidled close to her along a branch. Her mate returned at this time and the first-year male flew away. In another instance on the Vilas Park feeding ground (July 29, 1948) an adult female repulsed and then drove off a first-year male as he attempted to approach her. When the same female was approached by adult males she dropped one wing to the ground and moved away.

The first-year males also attempted to approach young of the year in a manner suggesting a sexual motivation. On numerous occasions at Vilas Park in June and July, 1948, first-year males were seen attempting to approach juveniles (as well as females) from the rear. The males were possibly attracted to the young by the latter's begging posture which greatly resembles the pre-copulatory posture of the female. On nearly all attempts they were repulsed, even by the youngest birds which seemed to recognize the first-year males as readily as did the females. Several times juveniles were seen to beg food from adult males and immediately afterward repulse first-year males. Even the juveniles assumed the bill-tilting posture when repulsing first-year males. In some cases first-year birds succeeded in mounting young. On July 8, 1950, a young bird begged to a first-year male three times and each time the young male mounted the juvenile and fluttered his wings overhead as if in attempted copulation. The first-year male in this case had held a kernel of corn in his beak. Somewhat similar behavior was observed on other occasions and could presumably have induced begging.

THE FEMALE "TERRITORY"

Female Territorial Behavior.—The activities of an established female on the marsh are largely within her mate's territory, owing mainly to the aggressive responses of neighboring males. (Alien mated or paired females usually draw only antagonistic responses from resident males; see Nero and Emlen, 1951). I have only one record of an adult male "courting" an alien, mated female and this occurred under experimental conditions. A female which had eggs was placed in a cage in a distant territory for 20 minutes and then given a slow release (June 1, 1950). Instead of immediately flying away as usual, she slowly walked out, drank and fed. The territory

owner approached her at once, with fully extended wings, stopping only to drive off his chattering mate. The female paid little attention and soon left. One of the main activities of the female is the aggressive defense of an area (with song-spread, bill-tilting, and attack) against intrusion by other females. Female intolerance of other females, however, varies considerably. At first, females often attempt to defend a large portion of the male territory, but as breeding progresses their attention turns more to the nest and to a much smaller surrounding area. By the time females have eggs in the nest they usually have developed a mutual tolerance over most of the male's territory, although the nest-site is still vigorously defended. Linford (1935) seems to have been the only previous author to describe "territoriality" in the female Redwing. He noted that each female claimed an area around her nest which she defended from other females.

Usually newly-arriving females establish territories without too much opposition by resident females. In large male-territories, where there is more room for subdivision by females, quarreling may be slight; in smaller male-territories female quarreling may be more pronounced. This is presumably the situation that Linford (*op. cit.*) observed. He stated that in a large male-territory the outlines of the female ". . . sub-divisions will be rather vague; but if it was small, then they will be sharply defined." Sometimes in the early stages of female territory development, intolerance of females is so general that other females have difficulty entering a male's territory. New females occasionally forced their way into a territory by persistence, threat, and actual fighting. The male often interferes in such disputes, invariably attacking his original mate. In one case (June 12, 1950) interference by his mate, which was just beginning to build a second nest, caused a male to lose a new female which had just appeared on his territory. While he was engaged in driving his mate far from his territory, the newly-arrived female was attracted to an adjoining territory by the resident male which had courted her from along the territory boundaries. However, in another case (April 18, 1950) a female which had arrived only the previous day drove a new female off of the male's territory several times, while the male looked on without interfering. The new female persisted in returning to the territory, however, and finally located there.

Nest-moving experiments (Nero and Emlen, 1951) showed that even after a mutual tolerance was developed between intra-harem females, actual visits to the nest were repulsed. Females from neighboring male-territories were actively repulsed at first, but later a partial mutual tolerance developed.

FEMALE TERRITORIALITY IN OTHER ICTERIDS

Similar territorial behavior in females has been noted in the highly-

territorial Yellow-headed Blackbird (Fautin, 1940:81-82). "The females seemed to exercise dominion over a small area immediately surrounding their nests but did not recognize the boundaries of the male's territory in which they nested. . . several females nested in the same male's territory, and although the different females in a few cases constructed their nests less than a meter apart, yet they were generally intolerant of each other in the vicinity of their own nests and more frequently occupied opposite extremities of the same male's territory. . ."

In the Brewer's Blackbird (*Euphagus cyanocephalus*), in which the male territory is loose and mainly connected with individual nest site and adjacent perches, the females "lay claim" to nest sites before actual construction begins (Williams, 1952:12). Aggressive activity for the possession of a nest-site ". . . is frequently prolonged and often acute and is largely carried on by females." According to Lack and Emlen (1939:226), in the highly-colonial Tricolored Redwing (*Agelaius tricolor*) ". . . the females usually ignored each other, but occasionally chased each other short distances." In Wagler's Oropendola (*Zarhynchus wagleri*) the males show no territoriality but accompany the females as the latter move about in small groups selecting their nest-sites. There is considerable quarreling among females over these sites (Chapman, 1928:138-140). Female Boat-tailed Grackles (*Cassidix mexicanus*) build in colonies apart from the males, which play no part in the nesting activities and remain in flocks (McIlhenny, 1937:278-282). No mention is made of inter-female tolerance at the nest-sites, but an island 34 feet by 32 feet was found to contain 34 nests.

TERRITORIAL SITE SELECTION AND CHANGE OF MATES

The nest-sites selected in successive years were recorded for 16 marked females. Nine of these returned for three seasons, four for four seasons, and one for five seasons. These records showed that females frequently nested in different places in successive seasons. The relocation distance of 30 nest-sites (Table 1) ranged from 4 feet to 240 feet (average, 65). These shifts caused some change of mates. On 10 occasions seven females mated with other males even though their former mates were present on the marsh. These females moved from 16 feet to 240 feet (average, 98; see Table 1). Nine females mated with the same male two years in succession, and two of these nine mated with the same male in three successive seasons. Change of mates was largely due to female movements since males returned to the same approximate area year after year. Of the six males whose females relocated and mated with other males, one made a territory shift of 80 feet (center to center); one remained in the same place but showed a slight decrease in territory size; one remained in position and showed an increase

in territory size; and three held territories with approximately the same boundaries as in the previous year.

In one case a female which had already chosen a nesting area and which had been there for two weeks suddenly moved to another territory to nest, even though a male was available on the first territory. A male was removed from his territory on May 12, 1950; the next day a neighboring male moved into the vacant territory, thus expanding the latter's holdings. One of his females, which had not yet nested and which he was actively courting, came with him. At the same time he showed an active interest in the resident female which had been present for 12 days: he flew to her again and again, gave song-spread, and remained near her. She persistently kept low in the vegetation as if to avoid him; after two days on the territory with him and his mate, she gradually moved into a third adjoining territory against some opposition by its owner. She was finally accepted by the latter male and nested successfully in his territory.

Females sometimes built nests and even laid several times in different places before bringing off a brood. They sometimes kept within the territory boundaries of their mates, but often they moved beyond them. In 1949, a female twice nested unsuccessfully within one territory, and then moved to

TABLE I

RELOCATION DISTANCE OF 30 NESTS.

Each figure shows the distance from the nest-site of the same female in a previous year, except for A and F, in which one year is skipped. Figures in heavy type indicate cases in which females mated with other males even though their former mates were present on the marsh.

Females	1949	1950	1951	1952	1953
A	?	80			
B	20	40			
C		100			
D		66			
E	30	200	34	6	
F	100	180	40	?	100
G	24	6			
H	14				
I		76	10		
J			76	4	46
K			16	30	50
L			70	50	
M			46		
N			46	240	
O			160		

another territory 225 feet away where she nested successfully, and to which she returned the next season. Generally when females move across territory boundaries to renest they necessarily mate with new males. In one case, however, a female remained with her mate even though she nested on an adjacent territory (Fig. 3). In May, 1950, female I₁ deserted a completed nest for unknown reasons, and renested successfully in an adjacent territory (H), though retaining her original mate (I). Her encroachment was not observed by me but on at least one occasion I saw male H chase her. Occasionally female I₁ was joined by her mate; apparently the tolerance

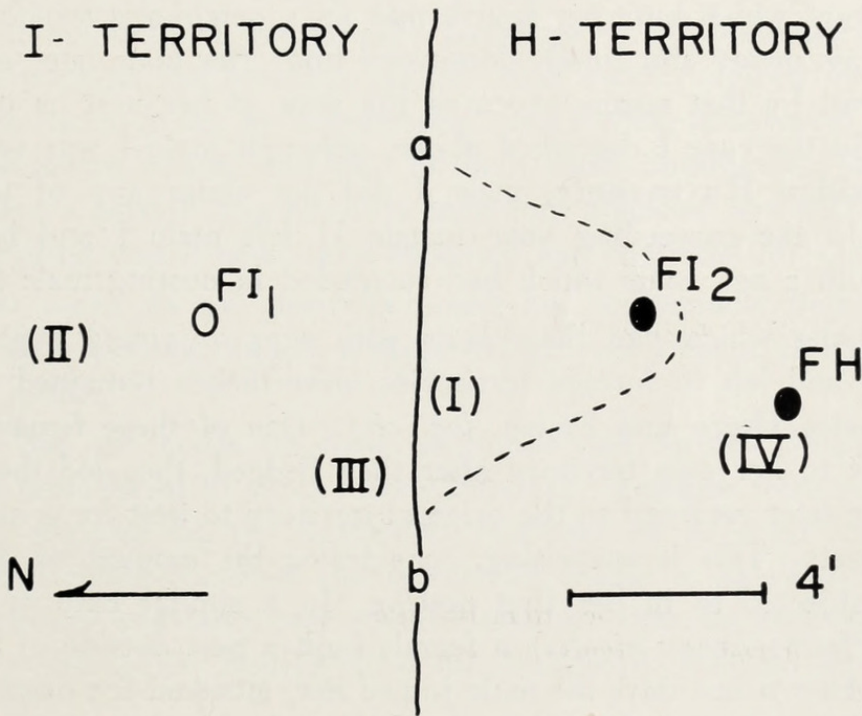


FIG. 3. Map illustrating boundary relationships after female renested in an adjacent territory. A female (FI) deserted her nest in I territory (FI₁) and renested in H territory (FI₂), placing a section of boundary *a-b* in questionable status. A caged young from the nest in H territory (FH), when placed at the positions indicated by Roman numerals in parentheses, drew the following reactions:

(I). Male I and female I remained on the area enclosed by the dashed line when female H first visited the area to feed her caged offspring, but only female I offered any resistance. One minute later male I withdrew before an attack by male H and both male H and female H occupied the area.

(II). Male H halted at line *a-b*; female H attempted to reach her young, but was routed each time by male I (and harassed by female I). Female H was unable to reach her offspring during 30 minutes.

(III). For 10 minutes female H was unable to reach her young. Male I remained perched between the young and its parents (MH, FH) facing them across the line *a-b*.

(IV). Male H and female H at once visited their young without any interference.

shown by the resident male to the intruding female was partly extended to the latter's mate. Results obtained from experimentally moving a fledgling showed, however, that the original territory boundary had not shifted and was recognized by both males. Hence the nest in question was actually located on a foreign territory.

This observation agrees with conclusions reached by experimental transportation of nests across territory boundaries. Under these conditions males accepted females which became familiar through repeated contact (Nero and Emlen, 1951:113). Somewhat similar observations have been reported in other species. Nice (1943:188), particularly, tells in detail how a female Song Sparrow, which built her fourth nest on a neighbor's territory, fought with the male owner and finally dominated him. Her mate later also fought the male and by that means procured the area of her nest as part of his territory. In the case I described above, although male I was occasionally tolerated within H's territory, male I did not claim any of the latter's territory. In the succeeding year female II left male I and bred on H territory with a new male which had succeeded in ousting male H.

Two females which had their nests with eggs or young experimentally transferred and left in foreign territories, nevertheless remained with their original mates (Nero and Emlen, *loc. cit.*). One of these females led her young back to her own territory after they fledged, then led them off the marsh. She later returned to the original territory to nest for a second time with her mate. This is surprising, considering the amount of disturbance she was subjected to in her first nesting. In a similar case in the Snow Bunting (*Plectrophenax nivalis*) a female built a nest outside of her mate's territory. After a few days the male joined her, attacked the original owner, and after two days' fighting seized the area in the vicinity of the nest (Tinbergen, 1939:31). On the other hand, in one extraordinary case, a female Redwing, which had already built a nest, deserted her mate when a second male stole a portion of the territory which included the nest site. The female stayed with the second male, brought off her young, and later returned for a second brood with her new mate (see p. 139).

Howard (1952:54-55) tells how one pair of Great Tits (*Parus major*) nested in a nest-box which was in the territory of another pair. They flew straight from the nest-box to their own territory, never perching anywhere else within the strange territory. Nest material was gathered out of the territory and neither the male nor the female ever uttered a note or displayed when the resident male visited their nest. The latter made no objection to their presence. "There *were* no boundary lines, for the strangers made no claim to land . . . all they wanted was the nesting box, for they had no suitable hole in their territory."

SUMMARY

Males established territories on the breeding marsh from which all Redwings except the mate, and sometimes other species of birds, were aggressively repelled. Returning males often held the same or nearly the same area year after year. The average size of the territories was about one-twelfth of an acre. Incomplete territorial behavior in migrants was shown by males settling for short periods in the tops of trees in non-nesting areas near the marsh.

When adjacent territories were held by former neighbors, aggression was minimal, but new males created considerable disturbance. Territory boundaries were well-defined and usually remained in approximately the same position throughout the breeding period. New males obtained territories by moving into vacant areas, by "challenging" and forcing withdrawal or eviction through persistent attack, and also through sheer dominance. In one case a male seized a portion of a territory including a female and nest. Throughout the breeding period new males appeared and contested for vacated areas.

First-year males do not generally breed, but occasionally they held territories for short periods, and to a large extent were treated as adults by the territorial adults.

Females met the males on their territories and formed "sub-territories" within the boundaries of their mate's territory. Females were restricted to the mate's territory by the aggressive reactions of adjacent males. Considerable quarreling occurred among females within a male's territory over female-territories and later over actual nest-sites. Females also showed some seasonal persistence in nesting-sites, but frequently changed sites, as well as mates.

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