

AN INVESTIGATION OF TERRITORIAL BEHAVIOR IN THE AMERICAN REDSTART UTILIZING RECORDED SONGS

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THE territorial behavior of the American Redstart (*Setophaga ruticilla*) has been studied by Hickey (1940), and in greater detail by Ficken (1962). Hickey has described this species as being "highly territorial," defending an area by song and formalized displays. Ficken has described the territory as being maintained during the breeding season with both sexes usually remaining completely within it; the male defends the area against other male redstarts. The objective of this investigation was to examine experimentally territorial aggression in male American Redstarts in relation to their breeding condition, the size of their territory, and the location of an encounter within their territory. The area and changes in size of redstart territories were also studied.

These factors and their effect on territorial behavior in other birds have been examined in a number of studies. The nature of encounters in territorial male Ovenbirds (*Seiurus aurocapillus*) varied as the breeding cycle of the birds progressed (Weeden and Falls, 1959). The fact that a territory is defended with increased vigor the smaller its size and the nearer the intruders approach its center has been recorded (e.g., Bremond, 1963; Armstrong, 1965). Evidence that territories are compressible but that a minimum size appears to exist has been presented by Huxley (1934) and more recent investigators have elaborated on his ideas (Tinbergen, 1957). Observations of the effect of these factors on the response of a territorial male redstart have been referred to in several studies (Ficken, 1962; Ficken and Ficken, 1965), but this particular aspect of redstart behavior has not previously been studied experimentally.

Several field studies have shown that tape-recorded songs and calls are stimuli sufficient to evoke behavior which normally occurs in response to the singing of another bird (e.g., Weeden and Falls, 1959; Stein, 1963). Bremond (1963) has stated that the reaction of a territory owner to a previously recorded song was immediate and definite; the bird would approach and sing near the loudspeaker.

MATERIALS AND METHODS

This study was conducted at the Patuxent Research Refuge, Anne Arundel and Prince Georges Counties, Maryland. The habitat consisted of areas with an understory of bushes and young trees 5-20 feet high with much herbaceous undergrowth. Such habitat has been considered typical for this species (Griscom and Sprunt, 1957; Ficken, 1962). Male redstarts on adjacent territories were recognizable as individuals by differences in color pattern, eliminating the need for color banding.

In the spring of 1967 two phases in the breeding cycle of the redstart were studied. One series of experiments was conducted from 24 April to 4 May before the males had acquired a mate (pre-mating); the second series, 10 May to 21 May, was run between the time a mate was acquired and the end of nest building (post-mating). In a study of courtship in the redstart, Ficken (1963) observed that "A female never left a male after she once remained for as long as an hour." Therefore, we considered a bird mated if a female was present in the territory of a male during the major portion of an observation period (i.e., one hour). In all cases this criterion proved to be a valid indication of subsequent and continued matedness of the male.

The redstart possesses two song types: an Accented Ending Song (A) and an Unaccented Ending Song (U) which apparently differ in motivation and function (Ficken and Ficken, 1965). Since an analysis of these song types by Ficken and Ficken (MS) showed that playback of the A-type song usually induced significantly closer approaches to the speaker than playback of the U-type song, an Accented Ending Song obtained from the Federation of Ontario Naturalists Warbler Record was used in all the experiments. The playback tape consisted of a six-minute sequence of six repeats of the song per minute. An Uher 4000 S portable tape recorder and a Nagra DH amplifier-speaker were used. The volume of the speaker was maintained at maximum level and could be heard 200 feet away by the observers; during all playbacks the redstarts were within 100 feet of the speaker.

Several days before the redstarts were expected to arrive at the Refuge, a pre-determined study area of approximately 20 acres was staked out. When a male redstart was first seen in the study area during phase I (pre-mating), it was observed for at least one hour and each tree that it flew into was marked. (Each bird sang from most of the trees it visited.) The marked trees were plotted on a sketch map of the area and the locations of encounters with other male redstarts were recorded. Each of the plotted points on the sketch map of the bird's activities was connected to all the other plotted points by a straight line. The area of the polygon thus formed was calculated with a compensating polar planimeter and will be referred to as the bird's maximum utilized territory. A redstart's activities appeared to be restricted to this specific area and it advertised its presence within it by singing. Although not enough territorial disputes were observed to state clearly that this entire area was defended in the strictest sense, all observed intrusions by other male redstarts were repulsed by the owner of the utilized territory.

In both the pre-mating and post-mating phases, the redstarts were observed during the playing of the stimulus tape in the center of each bird's maximum territory, and somewhere on the periphery of the territory. Approximately 24 hours separated the peripheral and center playback experiments for each bird. All the experiments were conducted between 07:00 and 11:00 EDT, and the time for each series of playbacks for a given bird was kept as constant as possible (i.e., within a range of two hours).

When a bird had moved into a desired location for a playback, the speaker was placed on the ground about 50-100 feet away from the bird. After the equipment was set up the bird was watched for six minutes, during which its vocalizations and distance from the speaker were noted. If the bird remained within 50-100 feet of the speaker during this period, the six-minute stimulus tape was played. After each stimulus song the location of the bird in relation to the speaker was noted as were his vocalizations. The next day before an experiment was initiated, the bird was observed for 30 minutes to be sure no changes in territory size had occurred and that the bird had not acquired a mate.

During phase II (post-mating), the movements of the male redstarts were observed for approximately an hour before the first playback was conducted and shifts in the shape

TABLE I
APPROACH LATENCY

Bird	Pre-mating		Post-mating	
	Periphery	Center	Periphery	Center
A	(>36)*	(>36)*	24	16
B	6	13	23	29
C	33	11	19	4
D	10	5	(NE)**	(NE)**
E	13	4	8	6
F	9	12	17	12
G	31	4	16	15
H	(>36)*	(>36)*	(>36)*	(>36)*
I	6	9	3	10
J	1	2	2	8
K	(NE)**	(NE)**	4	3
Median	11.5	10	16.5	11
60 percentile	6-33	4-13	4-23	6-16

* No approach within 30 feet during 36-song playback experiment.

** No experiment performed.

No significant differences between paired comparisons.

and maximum size of the territory were noted. The peripheral and center playback procedure in this set of experiments was the same as that used during phase I (pre-mating).

During the course of the six-minute playback, a reactive redstart would fly toward the speaker usually giving some type of vocalization. The bird would approach the speaker in an ambivalent manner, moving closer and then farther away, occasionally flying over it. The exact nature of the response was variable: some birds would approach the speaker almost immediately, others would not; some would sing each time the stimulus song occurred, while others were considerably less vocal. Therefore, three criteria of responsiveness were used: the number of songs played back before the bird approached within 30 feet of the speaker (approach latency), the number of songs played back during which the bird was within 30 feet of the speaker (approach duration), and the number of times a bird flew over the speaker divided by the number of songs played back during which the bird was within 30 feet of the speaker (flights over speaker). The criteria, flights over the speaker was handled this way in order to maintain the independence of the three criteria. In other playback studies, variants of these criteria have been utilized (e.g., Weeden and Falls, 1959).

With the use of the Wilcoxon matched-pairs signed-ranks test, a comparison was made between the birds' responses to peripheral playbacks and their responses to center playbacks. The data obtained during pre-mating and post-mating were treated separately and a comparison of peripheral versus center responses was carried out for each criterion.

RESULTS

Measures of responsiveness.—The data for the redstarts' responses are shown in Tables 1-3. Eleven birds were tested: nine birds were tested during pre-mating and post-mating; one was tested only during pre-mating (it

TABLE 2
APPROACH DURATION

Bird	Pre-mating **		Post-mating	
	Periphery	Center	Periphery	Center
A	0	0	7	10
B	16	24	9	8
C	4	6	4	29
D	20	27	(NE)*	(NE)*
E	4	6	29	6
F	4	16	3	8
G	6	21	13	22
H	0	0	0	0
I	12	6	20	12
J	12	24	35	27
K	(NE)*	(NE)*	33	34
Median	5	11	11	11
60 percentile	3-12	6-24	4-29	8-27

* No experiment performed.

** $0.05 > p > 0.02$ (Other paired comparison not significant.)

TABLE 3
FLIGHTS OVER SPEAKER

Bird	Pre-mating **		Post-mating	
	Periphery	Center	Periphery	Center
A	0	0	0.14	0.20
B	0.06	0.08	0.22	0.25
C	0.25	0.33	0.25	0.14
D	0.20	0.56	(NE)*	(NE)*
E	0.25	0.17	0.17	0.17
F	0.50	0.63	0.33	0.38
G	0.17	0.33	0.15	0.09
H	0	0	0	0
I	0.17	0.50	0.10	0.08
J	0.67	0.79	0.34	0.30
K	(NE)*	(NE)*	0.12	0.24
Median	0.185	0.33	0.16	0.185
60 percentile	0.06-0.25	0.08-0.56	0.12-0.25	0.09-0.25

* No experiment performed.

** $0.05 > p > 0.02$ (Other paired comparison not significant.)

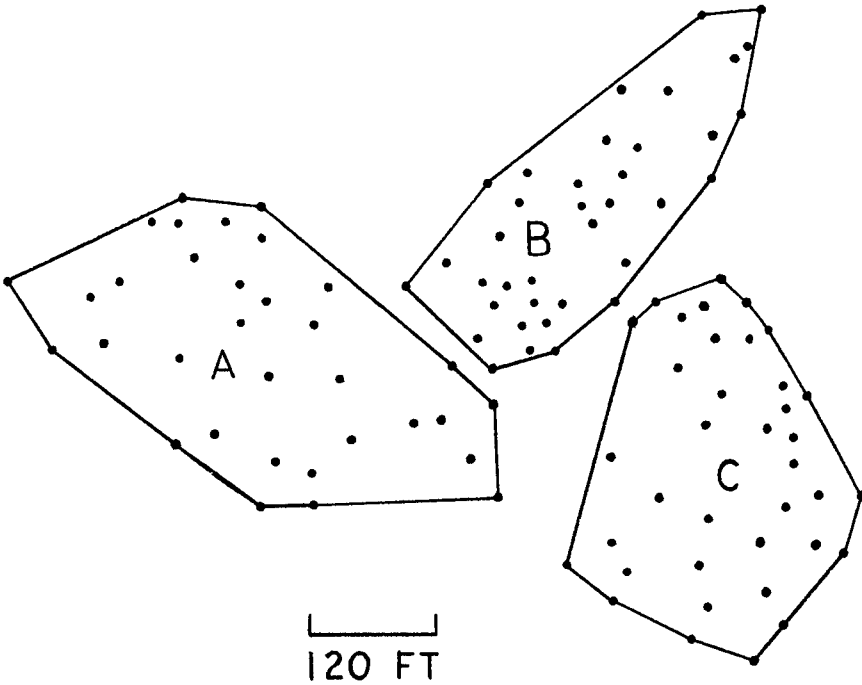


FIG. 1. Sketch map depicting maximum territories of unmated birds (pre-mating). The letters denote the birds identified in Tables 1-4. The black dots represent the trees a redstart visited during the one-hour observation period.

abandoned its territory and another bird was substituted and tested only during post-mating).

The data for approach latency (Table 1), showed no significant difference between the responses to peripheral and center playbacks either during pre-mating or post-mating. During pre-mating there was a significant difference in approach duration ($0.05 > p > 0.02$) between the birds' responses to peripheral and center playbacks. They remained within 30 feet of the speaker for a longer period of time during the playbacks in the center of their territories. Similar results were obtained for the flights over the speaker criterion (Table 3). During pre-mating there were slightly but significantly more ($0.05 > p > 0.02$) flights over per unit time in response to center playbacks compared to peripheral playbacks. During post-mating there was no significant difference between the responses to peripheral and center playbacks either in approach duration or in the number of flights over per unit time.

Maximum territory size and shape.—Figures 1-2 are examples of the

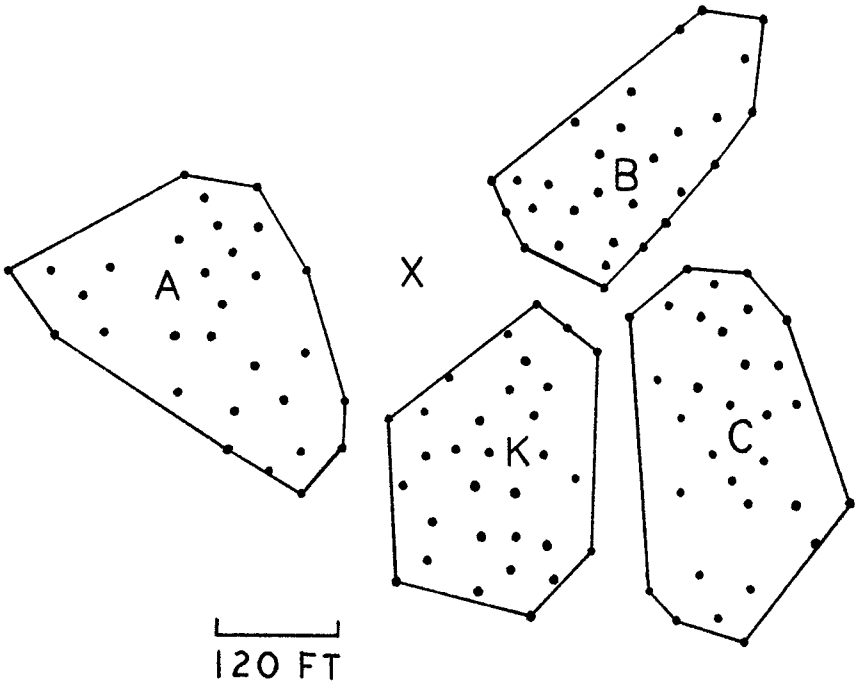


FIG. 2. Sketch map depicting maximum territories of mated birds (post-mating). The letters denote the birds identified in Tables 1-4. The black dots represent the trees a redstart visited during the one-hour observation period. The X indicates the approximate area occupied by a very late arriving bird not considered in this study.

sketch maps which show the territories the male redstarts held, and the territory size of each bird before and after mating is given in Table 4. The mean size before mating was 1.49 acres, and after mating was 1.13 acres. For six birds the territory size before mating was larger than after mating, the size of one bird's territory increased after mating, and in two birds there was no observed shift in territory size. The mean amount of shift in territory size for these nine birds was -0.32 acres.

DISCUSSION

Before a redstart acquired a mate, there was a significant difference between the defense of a territory's periphery and its center in two of the approach measures of responsiveness. The approach responses of the male in the center of his territory were more aggressive than those in the periphery (i.e., he remained near the speaker longer and flew over it more often per unit time in the center). However, between the time of pair formation and

TABLE 4
TERRITORY SIZES

Bird	Size before mating acres	Size after mating acres	Amount of shift in size acres
A	1.24	0.84	-0.40
B	1.57	1.29	-0.28
C	1.97	1.32	-0.65
D	1.77	*	—
E	2.01	1.41	-0.60
F	2.26	1.45	-0.81
G	1.17	0.92	-0.25
H	0.66	0.77	+0.11
I	1.00	1.00	0
J	1.24	1.24	0
K	*	1.09	—
Mean	1.49	1.13	-0.32

* No observations.

the end of nest building (post-mating), the redstart defended the periphery and the center of its territory about equally. Table 2 suggests that post-mating responsiveness is more like the intense pre-mating responsiveness at the center than the less intense reactions at the periphery.

The fact that a bird will defend its territory with increased vigor the nearer an intruder approaches its center has been noted on a number of occasions (e.g., Lorenz, 1938; Bremond, 1963), and this might be the type of reaction observed in this study. However, this does not explain why the redstarts were more aggressive in the center of their territories during pre-mating, while they defended the periphery and center of their territories equally during post-mating playbacks.

If redstarts normally spend more time in the center of the territory than in the periphery, the observed difference in response could be due to something completely unrelated to the playback experiments. There have been some observations made concerning any normal tendency the redstart may have to remain in either the center or periphery of its territory. The redstarts observed by Hickey (1940) seemed to move back and forth in an indefinite and irregular pattern covering the extent of their territories, and Ficken (1962) has stated that early in the season redstarts "seem to spend no more time at the center than at the periphery" of their territories. The sketch maps of the unmated birds observed in this study (e.g., Figure 1) seem to illustrate this lack of a preference for the center of a territory in the redstart. The locations a bird visited and sang from were distributed evenly between the center and periphery of its maximum territory.

Perhaps the redstarts were more aggressive in the center of their territories

because of previous experience in these areas. Morse (1966) found that the locations of past encounters were an important factor in determining what type of song Yellow Warblers (*Dendroica petechia*) would sing in particular parts of their territories. If the redstart's maximum territory is composed of a number of small areas which will differ in their importance to the bird based upon earlier experience there, the bird's responses to playback in different areas would be dependent upon the history of the bird's relation to its territory. However, it is unlikely that a bird's past experience in a given area was the main reason for the difference in aggressiveness observed in this investigation. The possibility of playing the stimulus tape in a locality of little importance was reduced by selecting areas for playback experiments in which the redstarts had been seen frequently during the one-hour observation periods. Also, the pre-mating playbacks were conducted very early in the season which minimized the effect of past experience on the playback experiments.

The breeding condition of the bird would probably have its effect on territorial behavior. A decrease in territory size might also produce changes in territorial behavior. Huxley (1934) has stated that territories are like "rubber discs"; the more they are compressed, the stronger becomes their resistance against further compression. Furthermore, these two factors may be correlated. All the birds with the largest territories (1.6–2.3 acres) were unmated; four of the five birds with the smallest territories (0.8–1.1 acres) were mated. Of the seven birds whose territory size was known during pre-mating and post-mating, six showed a decrease in size after acquiring a mate (Table 4). Apparently, the size of a redstart's territory is less during post-mating than before a mate is acquired. Although a causal relationship does not necessarily exist, there does appear to be a correlation between territory size and breeding condition. Therefore the effect of these two factors on the redstart's responses to playback could not be separated. In order to define more carefully the role of each of these factors in the redstart's defense of its territory, a larger sample size would be needed with a number of birds in the same stage of the reproductive cycle occupying different sized territories.

During the course of this study each redstart was not observed every day; therefore, the exact date each territory decreased in size could not be determined. It is possible that some of the territories were compressed before the females arrived and in these cases there might not have been any relationship between matedness and territory size. Assuming the territory size would have decreased regardless of the bird's breeding condition the "rubber disc" theory would apply to the redstart's equal defense of its entire territory after this decrease. To determine if this compression of the redstarts' territories

and not their breeding condition was the reason for equal defense in both the center and periphery, a number of birds would have to be continuously observed and the territory size recorded daily.

It appears that the problem of analyzing the redstart's territorial behavior utilizing a playback technique is considerably more complex than initially anticipated. The factors which help to determine this bird's aggressive activities appear to be interacting in a number of ways and are quite difficult to isolate.

The observed shifts in territory size and shape noted in this study appeared to be caused by several factors. The territories of Birds A, B, and C (Figs. 1-2) were reduced at least in part by the addition of late arriving males. In two cases first-year males were able to overcome the aggressiveness of the original territory owner, acquire some of his territory, and obtain a mate. In the only instance where a redstart increased the size of his territory after mating, the location of the female's nest appeared to determine the final size and shape of the territory. Apparently the female has ultimate control over the location of the territory boundaries and if she chooses to nest outside the male's original territory, the male expands his territory to include the area around the new site (Ficken, 1962). In two of the birds there were no noticeable differences in their territory sizes before and after mating. This seemed to be due to the limitations of the area where they first arrived; during pre-mating they were bounded by roads and neighbors on all sides.

The shifting of territorial boundaries in the American Redstart has been observed by other investigators (Sturm, 1945; Ficken, 1962). In this study the upper limit of population density probably was not achieved; denser populations were accommodated by a compression of territories (e.g., the area occupied by three birds during pre-mating (Fig. 1), was supporting five birds during post-mating (Fig. 2)). Several other ways territorial birds might accommodate a denser population are: (a) expand into less suitable habitats, (b) allow the territories to overlap (Weeden, 1965), and (c) increase the vertical foraging range (Ficken, pers. comm.). The redstarts studied here did not appear to utilize any of these other methods.

SUMMARY

Territorial behavior in the American Redstart was investigated by playing a recorded redstart song in the center and on the periphery of a male bird's maximum utilized territory. The bird's responses to the playbacks were observed and analyzed in order to determine what effect breeding condition, size of territory, and location of playback have on territorial defense. One series of experiments was conducted before a male had acquired a mate; a second series was run after a mate had been acquired.

During pre-mating the center was defended more vigorously than the periphery; during post-mating the center and periphery of a territory were defended equally. Some of the factors that might have been interacting to bring about this differential aggression were

discussed with no definite decision reached as to which were the most important; however, there was sufficient evidence to suggest that the redstart's past experience and normal activities were not particularly relevant.

The maximum territory of a redstart appeared to shift in size and shape between the time a male arrived and the end of nest building; usually a decrease in size occurred.

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