AGONISTIC BEHAVIOR AND TERRITORY IN THE AMERICAN REDSTART

MILLICENT S. FICKEN

THE purpose of this study is to describe the agonistic behavior of the American Redstart, *Setophaga ruticilla*, and to interpret this behavior from an ethological standpoint, *i.e.*, in terms of its causation, function, and derivation. In addition, individual distance and territory are discussed.

METHODS

A few essential terms are reviewed. *Agonistic* behavior is concerned with attack and escape. *Individual distance* "is an area around a bird, which moves with it, has no topographical reference, and into which no other individual is allowed to come" (Conder, 1949). *Displays* are defined by Moynihan (1955) as "those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers." Blest (1961) describes *ritualization* as "the evolutionary process responsible for the existence of inter- and intra-specific signalling movements." *Intention movements* are the "incomplete and low intensity movements, so called by Heinroth because they reveal what the animal is 'intending to do' . . ." (Marler, 1956). *Tendency* is used here in the sense of Hinde given by Marler (1956) as the "readiness to show a particular type of behaviour as observed under natural conditions."

The strengths of the attack and escape tendencies are determined by using the methods described by Tinbergen (1959). The first method involves recording what behavior follows a given display if the stimulus situation (*i.e.*, the other bird) remains constant. This method requires many observations of the same display since the stimulus situation often varies in natural encounters. If a display leads to attack 70 per cent of the time and to escape 30 per cent, it can be said that this display is caused by a relatively strong attack tendency in conflict with a weaker escape tendency. Another method involves an analysis of the situations in which the display occurs and is frequently used in this study in combination with the first method. The least reliable method consists of analyzing the form of the display. For instance, if it consists mainly of intention movements to fly from the opponent, one can postulate that it reflects a strong escape tendency.

The function of a display is determined by observing the response of the other bird (Tinbergen, 1959). For example, if a certain display by one bird typically causes the second bird to flee or to cease an approach, the display has a threat function.

The derivation of the components of each display is also discussed. Many of these elements, although exaggerated and otherwise modified during the course of evolution, are recognizable because the unmodified precursor is also performed by the species (Daanje, 1950). Thus the Neck Stretch display is probably a "frozen" intention movement of flying upward, since the birds perform a similar movement in nonconflict situations when they are merely flying upward. However, as a display it has become exaggerated in form and has a longer duration.

The redstart is an ideal subject for the study of agonistic behavior because its abundance in the study area results in frequent territorial encounters. In addition, the species is sexually dichromatic, tame, and usually nests low. Most males on adjacent territories were recognizable as individuals by differences in color pattern, eliminating the need for color banding.

Reproductive behavior was studied in the wild at Renwick Bird Sanctuary in Ithaca, New York. Investigations began in 1957 and were continued through 1959. A pocket tape recorder (Mohawk Midgetape) was used during part of the 1959 field season and was very useful for recording the more rapid interactions. Three or four pairs were studied intensively every year, and more casual observations were made on other pairs. In addition to studies in the field, five birds (two hand-raised from six days) were studied in captivity.

AGONISTIC POSTURES AND DISPLAYS

The postures and displays are grouped in three categories: aerial, nonaerial, and vocal. Before discussing agonistic displays that reflect the presence of both attack and escape tendencies, the acts of attacking and escaping are described.

Attacks proceed in different ways, depending on the position of the opponent. If the opponent is nearby, the attacker simply lunges at it. This almost always leads to the opponent's escape. In captivity, if the opponent does not immediately flee, the attacker often pecks it. However, pecking was never observed in the wild, probably because the opponent has a chance to flee. If the opponent is some distance away, as in many territorial encounters, the attacker first sleeks the feathers (a flight-intention movement) and then flies directly toward it. Escape is generally preceded by sleeking of the plumage and involves a flight away from the opponent.

Aerial Displays

Circling. These displays are horizontal and semicircular, or nearly circular, in form. The male flies out toward his opponent, and as he nears the other bird, often to within 30 cm (1 foot), he turns and flies back to near his original position. Occasionally the Circling bird flies behind instead

TABLE 1
REACTION OF THE OPPONENT TO CIRCLING

Acts	*Number of observations*
Chases other	20
Circling	17
Leaves	13
Fight	11
Remains (no display)	3
Titi	2
Chip	2
Muted Song	2
Song	1
Tail Spread	1

of in front of the opponent. As Hickey (1940) noted, the flight toward the opponent is often made with stiffened wing beats, but the return flight is apparently normal, or more rarely ends with a glide. There is generally no vocalization associated with Circling, but Bill Snaps were given by the displaying bird on two occasions. Circlings often alternate, and as many as 15 uninterrupted Circlings were observed with perfect alternation of the two birds. As soon as one bird completed the circle, the other flew out. Sometimes Chases are interspersed. Circlings are most frequently given by males and occur at territory boundaries. Occasionally a bird Circles into the middle of another's territory. This occurs when the displaying bird has "won" most of the boundary encounters with the other bird or when his female is in the other's territory.

Although Circlings occur between unmated males, they are more frequent after the females arrive. They become infrequent once the nest is built, as do all types of territorial encounters. Females occasionally Circled at me when I was near the nest, and on one occasion when a model female was placed near the nest. Fights followed Circling in 11 out of 18 cases. In seven other instances the bird performed acts (Chips, Muted Song, *Titis*) indicating a relatively strong escape tendency. The location of performance (the boundary), the form, and the acts that follow Circling indicate a slightly stronger attack tendency than escape, but both tendencies are evidently strong. Hickey (1940) and Benson (1939) have pointed out that this display probably has a threat function. The reactions of the opponent to Circling are shown in Table 1. He remains motionless as the Circling bird approaches, but often Chases him as soon as he turns for the return trip. The Circling bird was never Chased as he approached the other. Thus, only the first part of the display (Circling toward) functions as a threat. This display apparently does not have a very strong threat valence since the other bird usually does not leave and often initiates Fights and Chases.

This display may have originated from an attack flight toward the

opponent, but as the bird approached the opponent his escape tendency decreased and he turned and fled. However, during the process of ritualization the motivation may have shifted somewhat so that the display now reflects an attack-escape conflict with a somewhat stronger attack than escape tendency.

The stiffened wing beats are probably ritualized, reflecting hesitancy to approach the opponent. The glide away from the other bird may indicate thwarted fleeing. The fact that the bird arcs toward the opponent rather than flying directly at him probably reflects hesitancy to approach, and on the way back a hesitancy to return.

This type of boundary display was also reported by Kendeigh (1945) for the Magnolia Warbler (*Dendroica magnolia*) and the Black-throated Green Warbler (*Dendroica virens*).

Gliding. The bird Glides with wings outstretched and tail spread, sometimes with a few, small-amplitude wing beats, three to seven meters (10 to 20 feet) before alighting.

This display is performed only by males and is frequently given immediately following territorial encounters (particularly Chases and Fights). It is generally performed by the first male that leaves the conflict area as he flies away from his opponent and heads into his own territory, although on one occasion a male Glided as he was pursuing another male. The bird usually performs no agonistic behavior immediately after Gliding but feeds or performs other maintenance activities.

Mutual Gliding, seen only five times, consists of slow Gliding of two males close together with one slightly behind the other. The birds Glide in circles about two meters (six feet) in diameter. In two cases such Gliding was followed by Fights, once by males returning to their respective territories, and twice by Circling and Chases. Mutual Gliding occurs only after prolonged boundary encounters when neither bird leaves the area.

It is difficult to assess the function of this display since the other male usually gives no overt reaction, and after territorial encounters is usually not even present when the bird displays. However, Gliding probably acts as a deterrent to pursuits, since a Gliding bird is never chased, whereas a male flying away from an opponent without giving this display is often pursued.

Fights. Generally the birds first fly up together and then fly downward; the upward or downward phase is variably accentuated. They remain level with each other and seem to strike at each other with either the bills or feet. Occasionally the birds seem to lock together, but usually they strike at each other without making contact. No birds were stunned, nor were feathers ever dislodged. Various vocalizations are given during Fights (Table 2).

TABLE 2
VOCALIZATION DURING FIGHTS

Sexes involved	*Number of fights*	*Bill Snap*	*Song*	*Snarl*	*Titi*	*Chip*
Male–female	25	3	6	7	–	–
Male–male	66	18	4	1	2	1

Generally only two, but rarely three and even four, birds participate. On one occasion five birds, three males and two females, were involved, two males actually Fighting and three others hovering slightly above them. When one of these left, two more began Fighting. Table 3 indicates the frequency of multiple Fights and the sexes of the birds involved.

Fights are infrequent among unmated males but occur frequently both within territories and at their boundaries during the pre- and nest-building periods. Fights at boundaries are almost always preceded by Circling and Chases. Birds separated after a Fight often remain perched quite close together, then usually one bird leaves, is Chased, or more Circlings and Fights ensue. Prolonged agonistic encounters between male and female are uncommon, but encounters between males sometimes last for an hour. Fights involving more than two males occur when several boundaries overlap. Fights occur within another's territory when a female, often in search of nesting material, crosses into it and her male follows her. They also occur when a male approaches another's female on her territory. Except in these cases, an intruding male flees when the owner approaches.

It is usually difficult to determine which male initiates a Fight because of the great rapidity of its onset. Male–female Fights are usually initiated when the male makes a direct aerial approach toward his mate and she flies out to meet him. This is also the way most male–male Fights begin.

Fights indicate a strong attack tendency in both participants, although certain vocalizations indicate the presence of an attack-escape conflict. Fights in this species are somewhat ritualized, as evidenced by their form and general lack of physical contact.

Chases. Chases occur frequently at the boundary and within the territory when another male intrudes. In the latter case the owner flies rapidly

TABLE 3
BIRDS PARTICIPATING IN FIGHTS

Birds involved	*Number of observations*
2 males	66
1 male and 1 female	25
2 females	10
2 males and 1 female	6
3 males	3
3 males and 2 females	1
4 males	1

in its direction and the other turns and flees with the owner following. Chases usually stop at the boundary. If the boundary is crossed, the pursued bird usually turns and Chases the original pursuer out. The form of the Chase seems to depend on the course taken by the bird being pursued, and Chases at the boundary often involve several circles. In this case the bird being pursued does not have as strong a tendency to flee as when being Chased from another's territory.

Chases appear to be somewhat ritualized, since the pursuer rarely catches up with the pursued and often neither flies at top speed. In one instance the pursuer gained on the pursued and then the two birds flew side by side. Generally there are no vocalizations associated with Chases; but in one instance Bill Snaps were given, and in another, Snarls.

Nonaerial Displays

Crouch. This is the first agonistic behavior pattern of the young, appearing at about eight days of age. Crouching appears very suddenly, in contrast to many of the maintenance activities that have a gradual pattern of development. As in the Song Sparrow (*Melospiza melodia*) (Nice, 1943), this posture is only present for two or three days and disappears when the young leave the nest.

Crouching involves a retraction of the head and flattening of the body against the bottom of the nest. The birds often remain motionless for several minutes. This posture is given when the nest is jarred, in response to sudden noises and to the alarm Chips of the parents. The captive birds soon habituate to slight noises, and after a while only Crouch when there is a sudden loud noise.

This posture probably reflects a strong but thwarted escape tendency. If the bird is hungry and also fearful, it often adopts a compromise posture (Andrew, 1956b). The bird still Crouches but gapes as in regular begging.

Crouching is present at the time the young are most active in the nest, and despite its short duration, must have survival value in rendering them less conspicuous and thus reducing predations.

Freezing. This posture occurs in response to aerial predators in the wild, and in captive birds in response to sudden noises and the approach of a cat. Body feathers are sleeked, neck elongated, body held horizontally, and eyes bulged.

The bird is generally motionless but sometimes makes quick sideways movements of the head. On one occasion two captive birds remained motionless for 2.5 minutes after a cat had left, then the feathers returned to their normal position and finally the birds moved their heads and peered around. Only after five minutes did a bird change the position of its body.

Marler (1956) describes a similar posture that is adopted under the same conditions by the Chaffinch (*Fringilla coelebs*). This posture also occurs in many other species. Marler states that, "The 'freezing' posture is thus built up mainly of flight intention movements that prepare the bird for sudden flight and also assist in concealment." This posture is evidently motivated by strong fear.

Pivoting. This posture consists of sideways movements of the body through an arc of about 60°. The feet do not change position. These movements, accompanied by Chips and Tail Spread, are associated with the mobbing of Common Grackles (*Quiscalus quiscula*) and a Cooper's Hawk (*Accipiter cooperii*). Pivoting is performed at least six meters (20 feet) away and facing the animal or object causing the conflict. It is frequently performed by females at some distance from the nest during egg laying and incubation, but is never observed during the parental phase. Following pivoting the female usually flies to the nest. This posture is also adopted by males watching their mates during the courtship period. In these instances, approach toward the female ensues about as frequently as remaining or flying away. Occasionally, it is performed after territorial encounters, and the bird then leaves the area but soon returns.

This ambivalent movement evidently expresses a low balance of tendencies to approach an object or animal in conflict with an escape tendency or a tendency to remain. Andrew (1956a) describes a similar movement in *Emberiza* spp., but this differs in context from redstart pivots in that it is often performed by males near a rival. Pivots are given during mobbing by both *Setophaga* and *Emberiza*. Evidently a rival male does not produce the same conflict in *Setophaga* as does a potential predator.

Alert Posture. This posture consists of sleeked body feathers and upstretched neck, often with a Tail Spread. The bird constantly moves its head and peers in all directions. There is no vocalization except for an occasional Metallic Chip. The posture is assumed after any sudden noise disturbs the bird on the ground. It seems to express a conflict between fleeing (in this case flying upward) and remaining in position.

Neck Stretch. The bird elongates the neck, but the bill is not pointed upward as in similar displays of many icterids. The Neck Stretch was observed only in captive birds and was rare even in this situation. It apparently occurs only when individual distance is violated, which occurs far more frequently in a small cage than in the wild.

The dominant individual generally extends its neck higher than the other, who is generally the first to flee. The response of the opponent to a Neck Stretch is also a Neck Stretch, or more frequently, fleeing, indicating that this display has a threat function. Sometimes the displaying bird

gives a downward peck at the opponent if the other bird does not leave immediately, indicating a tendency to attack.

Head Forward. The bird turns on the perch and faces the opponent with contour feathers sleeked, body low and horizontal, neck outstretched, and (usually) gaping. The wings are in the normal resting position or just slightly drooped. Bill Snaps or Snarls are frequent.

This display is most frequently given by the female when her mate has just approached within a few meters of her, or after she approaches a female Brown-headed Cowbird, *Molothrus ater,* in the territory.

The Head Forward is somewhat different in form when oriented at a cowbird, because it usually incorporates the Tail Spread (indicating more fear). Her hesitancy to approach a cowbird very closely, unless it is near the nest, also indicates more fear of the cowbird than of her mate, who is often lunged at from this posture. In 16 cases when the bird gave this display and the opponent remained, the displaying bird fled in only five instances and gave other threat displays (Bill Snaps, Snarls) in 11 instances. In 19 instances, the male fled in response to this display and remained in only two instances, indicating a strong intraspecific threat valence. This display is less effective in causing a cowbird to leave.

The slim horizontal body, the elongated neck, and the position facing the opponent are intention movements of moving toward the opponent, and are probably indicative of a strong attack tendency. The gape is a ritualized biting movement. This type of display is found in many passerine species, for example, the Chaffinch (Marler, 1956), Song Sparrow (Nice, 1943), and thrushes of the genera *Catharus* and *Turdus* (Dilger, 1956).

Neck withdrawn Gape. This posture was observed only during the prenesting period when the male approaches the female and lands within 30 cm (one foot) of her and slightly under her. The neck is withdrawn, giving the bird a hunched appearance, and the gape is directed upward at the female. The gape does not appear to be as wide as when delivered from the Head Forward posture.

The fact that the male often flees after performing this display indicates that it expresses a stronger escape tendency than does the Head Forward gape. This is also indicated by the weaker attack components of the display and the fact that the male does not alight beside the female but remains below her. The female always Chips when the male employs this display, but she usually remains and the male flees. Thus, this display seems to have a rather weak threat valence, but does cause a slight increase in the escape tendency of the female as evidenced by her Chipping.

The withdrawn neck is perhaps derived from a flight intention movement, while the gape is basically an attack intention movement.

TABLE 4
TAIL SPREAD AS A DISPLAY COMPONENT

Usually accompanies	*Occasionally accompanies*	*Rarely or never accompanies*
Chip	Titi	Freezing
Distraction display	Bill Snap	Song
Head Forward	Wings Out	Zeep
Glide	Snarl	Neck Stretch
Alert		

Wings Out. The contour feathers are sleeked, the body held horizontal, and the bird faces the opponent. The wings are lifted horizontally out from the body, making the red patches at the base of the secondaries more conspicuous.

This display was performed only by males except on one occasion when a female directed it toward another female. It was observed only in territorial encounters and was usually given when the bird was 1 to 2.5 meters (three to eight feet) away from an intruder, following Chases or Fights. Occasionally, it occurred after the resident male had chased out the intruder. This display is confined to the territory, usually occurring well within it.

The acts performed by the displaying bird immediately following the display consisted of flying at the opponent in eight instances and of fleeing in only one instance. Thus Wings Out evidently reflects a stronger tendency to attack than to escape.

Wings Out leads to immediate flight of the opponent in some cases. However, in most instances the other bird flies only when the bird that has been displaying actually starts flying in its direction. This indicates that the display has a weak threat valence. However, it usually occurs after the intruding male has been chased or fought, indicating that it has a very strong tendency to remain.

The sleeked feathers and the horizontal body are flight-intention movements. The extension of the wings outward is probably derived from a flight-intention movement and expresses the attack tendency.

Tail Spread. The Tail Spread is the most common display of the redstart and is performed by both sexes in a variety of contexts. In addition to being performed alone, it is associated with many displays (Table 4). The rectrices are spread to various degrees while the tail is held level with the body, or in some cases, "cocked" upward.

Tail Spreading will be considered here only when it occurs with no other displays. The variety of behavior patterns preceding and following this display (Table 5) makes an analysis of causation difficult. It is given by newly captured birds when they are frantically trying to escape from a

TABLE 5
TAIL SPREAD

Acts preceding	*Number of observations*
Fight	15
Feeding	14
Chip	13
Chased other	7
Was chased	5
Circling	3
Titi	2
Pivots	2
Muted Song	2
Acts following (by the displaying bird)	*Number of observations*
Approaching other bird	26
Flees	8
Song	8
Chip	7
Fight	5
Muted Song	2
Pivots	2
Titi	1
Head Forward	1

cage, at a time when the attack tendency is probably low. On the other hand, it is given just before a Fight or Chase when the bird apparently has a strong attack tendency. It is also often performed between flights by a lone individual.

This display is apparently the result of a wide range of degrees of the escape tendency in conflict with another tendency, *e.g.*, to attack, in the case of territorial encounters; sex, in the case of courtship displays; to remain in the case of hesitancy by the female to approach the nest. Another indication that it expresses the escape tendency is that it is usually performed at the territory boundary and less frequently within the territory.

Tail Spread was performed while the bird was singing on only four occasions. In two instances the bird was giving Muted Song, and in two others the song was preceded by a series of subdued Chips, both of which indicate a stronger escape tendency than ordinary song.

The greatest amount of spreading of the tail and the greatest degree of "cocking" are present in male courtship displays and immediately following Fights by both participants when neither bird leaves. Cocking thus probably reflects a higher degree of conflict than do other positions of Tail Spread. It also seems to function as a threat, since other birds rarely approach a bird that has a Tail Spread.

The Tail Spread appears to be a ritualized flight-intention movement exhibiting the bright tail markings. Tail Spreading has been reported in several other warblers with patterned tails: *Myioborus miniatus* (Skutch,

1954); *Setophaga picta* (Bailey, 1913); and *Dendroica magnolia* (Kendeigh, 1945).

Distraction display. This was observed on two occasions. When I approached a recently fledged bird, the female flew to the ground near me, and moved away from me slowly, with tail spread, and wings outspread and quivered. A similar display was performed by a male near the nest, but he did not move about as much as did the female. Skutch (*in* Bent, 1953) also describes a male performing a distraction display near the nest.

Vocal Displays

Screech. The Screech first appears on the day the young leave the nest and is heard until the birds are about 40 days old. It seems to change in form so that it becomes similar to the Snarl, which is performed by adults. A similar vocalization in the Song Sparrow (Nice, 1943) appears a day or two earlier but disappears after the 14th day.

Recently fledged captive birds Screech when another steps on them and when they are handled. After Screeching the birds often gape at the offender and/or peck and bite him, indicating attack tendency. However, they occasionally flee, indicating that the escape tendency is present as well.

Screeches seem to function as a threat because they often cause retreat of the other bird when individual distance is violated.

Snarl. This vocalization, which has a hissing quality, is usually uttered in rapid succession. Snarls are given in the same situations as the Head Forward, and are often preceded by this display. Snarls are also given during Fights, and in direct flying attacks. The acts following a Snarl were direct approaches in seven cases, and fleeing in only one, probably reflecting a relatively strong attack tendency.

Snarls function as a threat since they cause fleeing, or at least a cessation of approach when given by the female as the male approaches.

Similar vocalizations are given in much the same context by such diverse species as the Red-eyed Vireo (*Vireo olivaceus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), and Cerulean Warbler (*Dendroica cerulea*).

Bill Snap. This display, like the Snarl, is frequently preceded by or performed during the Head Forward. It is given by both sexes in both inter- and intraspecific encounters. In those cases when it is given in the stationary Head Forward position, lunges usually follow if the opponent does not leave. Bill Snaps were frequently given during Chases (evidently by the pursued), during Fights, and during flying attacks on the opponent. Thus this display is indicative of a strong attack tendency and often accompanies attack.

There is often a rapid alternation of Snarls and Bill Snaps as the bird lunges at, or flies at, the opponent. Although this suggests that the two

displays are causally similar, there are some differences in the situations in which they are given. Bill Snaps occur frequently in male–male Fights, but only rarely in male–female Fights. Snarls are more frequent in the latter (Table 2) and are probably uttered by the female. Bill Snaps are sometimes given in male–male Chases, but Snarls are never heard in this context. The female often Snarls when the male approaches; Bill Snaps are usually not given in this context. Bill Snaps seem to express stronger attack tendency than do Snarls.

Bill Snaps have a strong threat valence and are given more frequently in offensive than defensive situations, but are sometimes given when other displays are not successful in driving off an opponent.

This display is probably a ritualized biting movement, noted in many passerine species, for example, the Chaffinch (Marler, 1956), thrushes of the genera *Catharus* and *Hylocichla* (Dilger, 1956), and the Bay-breasted Warbler (*Dendroica castanea*). However, it is lacking in most Emberizinae (Andrew, 1956a).

Zeep. This short, sibilant vocalization is performed more frequently by the female than the male during the breeding season. It is often given by the female during nest building and incubation when the male suddenly sings after a long silence. She also gives it occasionally as the male approaches but is still some distance away. It is also given during flight.

Zeeps are very frequently followed by flight but occasionally by remaining and by Harsh Chipping. These notes evidently express a conflict between flying and remaining.

Zeeps cause the male to approach the female in many instances and seemingly make the male aware of the presence and location of the female.

Chip. Redstarts have two Chip notes that could usually be distinguished with ease. However, in certain situations they grade into each other. The Metallic Chip, a sharp note, is given by both sexes in such contexts as the approach of a cat, mobbing, and occasionally in the alert posture. The female sometimes gives it when the male approaches her at the nest. Metallic Chips occur when a bird is struggling to reach an insect outside the cage, and also in birds that have just been caught and caged.

These Chips apparently express a strong escape tendency, either thwarted by physical factors (such as a cage) or by other strong tendencies such as to approach (in the case of mobbing), or, more frequently, to attack (in cases where the female Chips as the male approaches).

Such Chips are often repeated rapidly, *e.g.*, 13 in 10 seconds by a newly caught bird. At high rates the birds show much locomotory activity, constantly trying to escape from the cage, while at lower rates, locomotory activity is less. Thus a high rate of Chips seems to indicate a stronger escape tendency than do lower rates.

The Harsh Chip, a one-syllable note with a much harsher sound than the Metallic Chip, is typically more frequent in the female than the male, except during the parental phase. The female makes Harsh Chips when the male approaches near the nest and when her mate is involved in territorial encounters. She also gives them immediately after being chased by him. Chips are also frequently given as the female leaves the nest (and occasionally before an approach) during the nest-building period. Zeeps often precede Chips, and rarely Zeeps and Chips alternate.

The acts following Harsh Chips were other displays in four instances, approaching the other bird in nine, attacking in three, and fleeing in six cases. Harsh Chips seem to reflect an approximate balance of attack and escape tendencies.

The response of the male to Harsh Chips was: attack (1), Chips (12), approaches (46), and flees (64). Thus this display can function both to attract and repel the other bird. If the male is some distance off and the female gives one or two Chips, he often approaches to within about seven meters (21 feet). However, if the male approaches the female closer than this, she Chips many times in rapid succession, and the male then leaves. Thus the frequency of Chips seems to determine the reaction of the other bird. This vocalization has good carrying power and may serve to keep the male aware of the location of the female as well as inducing him to approach her. Females frequently respond to the Chips of females on adjacent territories by also Chipping.

Metallic Chips, Harsh Chips, and Tail Spread are all indicative of the tendency to escape. The Tail Spread occurs with both types of Chips and seems to indicate a wider range of strengths of the escape tendency than do the two types of Chips. Metallic Chips reflect a stronger escape tendency than do Harsh Chips.

Titi. This high-pitched vocalization consists of two or more syllables that sound like *titi* or *chichi.* The feathers are generally sleeked, making the bird appear very slim, the eyes are bulging, and sometimes there is a Tail Spread as the bird utters this vocalization.

Titis are most frequent in males, occurring at boundaries, and often precede song there even if the rival male is not nearby. Occasionally they are given by a male as he is being pursued by another, and also just after the bird lands after being chased.

Females sometimes gave this vocalization when I approached the nest, occasionally alternating it with Harsh Chips, and remained about one meter (three feet) away from me until I left the nest area.

The acts performed by the displaying bird following this vocalization seem to indicate a relatively strong escape tendency in conflict with a

weaker attack tendency or a tendency to approach. This is also indicated by the situations in which the display occurs, as well as the sleeked plumage and bulging eyes, which are found in other displays where escape is strong, particularly in Freezing.

Song. The ontogeny of song was not studied in detail, but observations were made on one male that had been hand raised from the age of six days. This male was first heard singing a muted, rather formless warble when 17 days old. At about two months of age he began singing loudly, but the song still consisted of disjointed warblings. A little later the song was modified, and the phrases were more like those of the adult. By five months of age he was producing songs of adult quality, including the typical ending. This developmental sequence is evidently common in passerines (Nice, 1943; Lanyon, 1960). Song was confined to the male in all individuals that I studied, but there are reports of females singing (Bent, 1953).

Three first-year males were studied, and all had songs differing in quality from those of older males. Borror (*in* Griscom and Sprunt, 1957) also noted this difference. Two first-year males had very "hurried" songs, but the song frequency (about eight per minute) was comparable to those of the older males. The other young male persisted in giving Muted Songs even after he obtained a mate, and only very rarely uttered a song of full volume. First-year males have songs of both types (see below).

The singing bird generally has the body feathers slightly fluffed and holds the head slightly back. There are usually no visual displays associated with song, although rarely wing quivering is performed by a lone singing bird.

Some parulids have flight songs differing from their regular advertising song (Bent, 1953). The redstart sometimes sings in flight but employs the advertising song. Song occurred in flight when a male was alone in the territory in two instances, after an encounter as he fled from the opponent in 15 instances, and as he swooped at the female in eight instances. Thus flight song differs in context from songs delivered from a perch.

The songs of the American Redstart have been described by Gunn and Borror (*in* Griscom and Sprunt, 1957) as follows: "The songs of this species are high pitched and somewhat lisping, and are subject to a great deal of variation; one bird may sing songs of several different types. The songs are of two general patterns; in one the song consists of 4–7 similar notes or phrases, with a louder and lower pitched note at the end; in the other the song consists of a series of 2–8 similar phrases, without the lower note at the end." The song with the distinctive ending will be referred to as Accented Ending Song and the other as Unaccented Ending Song.

The Accented Ending Song is performed primarily within the territory

TABLE 6
OCCURRENCE OF THE TWO SONG TYPES DURING THE NESTING CYCLE

Male	*Stage*	*Number Unaccented Ending Songs*	*Number Accented Ending Songs*	*Ratio Unaccented Ending to Accented Ending Songs*
E	Nest building	25	25	1 : 1
S	Nest building	35	25	1.4 : 1
S	Incubation	74	43	1.8 : 1
S	Parental	52	27	1.9 : 1

when there are no "disturbances" (*i.e.*, female nearby, intruding male). The Unaccented Ending Song was performed at the boundary and following encounters. After an encounter the bird usually sang a Muted Unaccented Ending Song followed by several Unaccented Ending Songs of full volume. Other than under these conditions, the two full-volume song types were generally performed during the same singing bout and were often alternated.

There is apparently seasonal variation in the performance of these two song types, involving an increase in the relative number of Unaccented Ending Songs as the nesting cycle progresses (Table 6). Benson (1939) also noted the preponderance of these songs during and after the molt.

It is difficult to ascribe motivations to song types, because they often alternate in the same bout. It is common to hear 20 or more songs and to find perfect alternation of the two types. This does not necessarily mean that the types do not have different motivations. After the bird has performed one song type, the threshold may be raised for the same type but lowered for the other. Hinde (1958) found that in the Chaffinch each song is more likely to be followed by a similar song type than by a dissimilar one. Thus in this species, unlike the redstart, there is, "a persisting tendency to repeat the song last uttered: this we may describe as a facilitative effect. This facilitative effect could be merely a consequence of slight differences between the motivational factors for each song type."

The Unaccented Ending Song probably expresses a weaker attack tendency (or stronger escape tendency) than does the Accented Ending Song, as indicated by its performance at boundaries and immediately following encounters, and its relative increase during the parental phase when the male shows few indications of the territorial aggressiveness so prevalent earlier in the season.

Muted or whispered songs are heard frequently. They appear to have the same form as regular songs but are delivered at a lower volume, varying from those scarcely audible a few meters away from the singing bird to those only slightly lower in volume than regular song. Both song types may be muted, although Muted Accented Ending Songs are rare.

TABLE 7
MUTED SONG

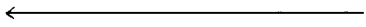
Acts preceding		*Acts following*	
Territorial encounters	33	Flees	8
Chip	10	Circling	5
Titi	2	Chase	3
Tail Spread	2	Pivots	2
Pivots	1	Approaches other	1
		Attack	1
		Chip	1
		Tail Spread	1
Situation			
At boundary	20		
Near nest	16		

Muted Song (Table 7) is probably indicative of a stronger escape tendency than song of normal volume since it is frequently given by both males after an encounter, near a territory boundary, and before approaching the nest, *i.e.*, in situations where the attack tendency is weaker. In addition, Muted Song is often preceded by Chips, *Titis*, and Tail Spread, all of which express a relatively strong escape tendency.

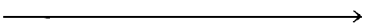
Song in the redstart is performed in many contexts but is limited to the territory during the breeding season, intruding males singing only Muted Songs or none at all. It is sometimes associated with direct attacks and often with Fights and pursuits of females, and, to a much lesser extent, males. Song is performed rarely during copulation, but it seems to have a different quality in this situation.

These songs apparently fall into a sequence leading from those expressing a stronger escape tendency to those with a stronger attack tendency. However, it was not possible to be sure of the relationships between Unaccented Ending Song and Muted Accented Ending Song. A tentative sequence follows:

Increasing Escape



Muted Unaccented Ending Song — Unaccented Ending Song / Muted Accented Ending Song — Accented Ending Song



Increasing Attack

As in most passerines studied thus far, song seems to have two principal functions, acting as a threat to other males and as an attractant to unmated females. Males rarely approach an area where there is a singing male, but they move into an area rapidly when the original male has left. Although song as well as visual displays delineate territory boundaries, song is the threat display that is effective at the greatest distance from the displaying bird and is thus ideally suited for territorial advertisement and threat.

During pair formation females may approach a male initially in response to his song, sometimes flying to him from as far as 100 meters away. However, once mated, females apparently are not attracted to songs of other males.

INDIVIDUAL DISTANCE AND TERRITORIALITY

Individual distance. Nestling redstarts constantly contact one another but show no agonistic behavior. Just after they leave the nest, however, they Screech when others contact them. Young birds perch close together without interactions until two months of age, when individual distance increases to include several centimeters around the bird.

A hand-raised male and female were caged together. They interacted very little until the male became sexually active at about three months. He then became dominant over the female, and agonistic encounters became more frequent as their individual distances increased.

Some displays associated with the defense of individual distance (Head Forwards and Snarls) are different from those occurring during territorial encounters (Circling and Wings Out). However, Tail Spread, Bill Snaps, Chips, and Fights occur in both situations, suggesting that territory and individual distance are causally related.

Territory. Hinde (1956) divides the behavior involved in territory establishment and maintenance into the following categories:

(a) Restriction of some or all types of behavior to a more or less clearly defined area.
(b) Defense of that area.
(c) Self-advertisement within the area.

The behavior of the redstart fits into this classification. The territory is maintained from the time of the male's arrival until fall migration, both sexes remaining completely within it except for occasional short wanderings, particularly by the female. The male defends the area against other male redstarts, while the female defends it against females. She also defends a smaller nest area against her mate as well as intruders of other species. Song is the means of self-advertisement and reduces trespassing.

Physical aspects of the territory. Benson (1939) states that the redstart "shows considerable adaptability in respect to nesting habitat, but most frequently seems to choose a rather moist deciduous woodland with plenty of second growth."

The study area, Renwick, encompasses about 16 hectares (40 acres) of such habitat. There were from 12 to 17 pairs breeding there. The birds were more concentrated in certain places that appear to be the areas with the most second growth between 1.5 and 6 meters (5 and 20 feet) high. There was also much herbaceous undergrowth in these areas. There is

TABLE 8
FIRST-YEAR MALES

Year	*Total number of males*	*Number of first-year males holding territories*	*Number of first-year males obtaining mates*
1957	15	0	0
1958	17	3	1
1959	15	2	1
1960	12	2	1

"edge" along a narrow road and some open areas. Such landmarks often form the boundaries of territories, very few encompassing both sides of the road or other open areas. No attempt was made to measure exactly the territory size, but the territories ranged from about 0.2 hectare (0.5 acre) to just over 0.4 hectare (one acre), averaging about 0.3 hectare (0.75 acre) when stabilized.

Inception of territorial behavior. Very little information is available concerning the behavior of the birds on their wintering grounds, but apparently there is none of the marked territorial behavior that occurs during the breeding season. Eaton (1953) observed that two to four redstarts frequently occur in flocks composed of several warbler species during the winter in Cuba. However, Skutch (*in* Bent, 1953) states that redstarts in Central America during the winter never associated with others of their kind. Redstarts do not sing while on their wintering grounds (Skutch, *in* Bent, 1953) but may sing just before the northward migration (Danforth, 1926).

Redstarts arrive at Renwick in the following order: two-year and older males, females, and finally year-old males. The older males, some of which are migrants, arrive the first week of May. The first females usually arrive about a week after the first of the males, and almost all of the resident females arrive within a week. Resident first-year males arrive about a week after the last of the resident adult males.

Records were kept of the location of the territories of the first resident males. Certain areas were usually occupied first, later birds taking territories on the fringe of these areas, while other areas were never utilized.

First-year males. Since first-year males are the last to arrive, they are left with the less favorable habitats. There are not any suitable undefended areas left in Renwick by this time. Later in the season, when boundaries shift, these males can sometimes shift into more suitable territories.

The first-year male population of Renwick is always small (Table 8), and this seems to be the case in other localities as well. Hickey (1940) reported four first-year males in a breeding population of 48 males in

Westchester County, New York. Sturm (1944) found that of 32 males only three were first-year males (two others held territories but did not secure mates). Kendeigh (1945) did not find any first-year males in a population of 10 males. Baker (1944) found a higher proportion of first-year males (two out of seven) in a Michigan study area, but his total number of birds was small.

The low number of first-year males may be due to any one of several factors: (1) Some individuals attain adult plumage at the postjuvenal molt while others do not. This occurs in the Olive Warbler, *Peucedramus taeniatus* (Webster, 1958). (2) First-year males generally do not breed and may compose a "floating" population. Kendeigh (1945) and Hickey (1940) report instances of wandering first-year males. The fate of the first-year females is unknown; it is possible that they also generally do not breed. (3) First-year males may breed principally in less studied parts of the geographical range.

Evidence is lacking to give definite support to any of these hypotheses, but the second explanation seems most probable. The problem certainly needs further investigation in many parts of the redstart's broad range.

Although no instance was noted of an older male failing to obtain a mate, first-year males are often unsuccessful (Table 8), probably because they usually arrive after all of the females are paired. Occasionally, a female straggles in late, weeks after most of the females, and becomes the mate of a first-year bird. The first-year males that fail to obtain mates remain on territories for about two weeks and then disappear.

Only two mated first-year males were studied through an entire breeding season. One of these had a territory of less than 0.2 hectare (0.5 acre)—the smallest territory of any individual studied. This bird was unsuccessful in expansion attempts and generally lost in boundary encounters. He usually sang Muted Songs. The other first-year male, however, had a territory of normal size and seemed as aggressive and successful in territorial defense as the older males.

Territorial behavior of unmated males. Males exhibit territorial behavior from the time of their arrival. Encounters before the arrival of females involve all the agonistic patterns associated with territorial defense except Fights.

Even when there is only one male in all of Renwick his territory encompasses less than 0.8 hectare (two acres). After a day or so the territory size decreases even in the absence of other males. When there are few males, there is often a gap of about 15 meters (50 feet) between territories. Later, many territories share a common boundary, probably due to population pressure, which seemingly causes a further, though slight decrease in size.

Redstarts do not have "singing perches" early in the season, but sing while foraging through the territory in a seemingly irregular manner. They seem to spend no more time at the center than at the periphery. Later in the season, however, they are more restricted in their movements.

Territorial behavior after the arrival of the female. Approximately 15 pairs were observed during this phase. The following account is based on their usual behavior. Relations between the male and female will be treated in detail elsewhere (Ficken, ms.).

The male's movements within the territory are affected by the female's movements immediately after her arrival. During her first day on the territory she follows the male, but then the male follows the female and stays near her until nest building begins. Initially the female spends one or two days wandering all over the territory. She seems aware of the territory boundaries very soon, but often crosses them while gathering nesting material.

Apparently the female has ultimate control over the location of the territory boundaries. She generally selects the first nest site within the territory. However, success of first nests is low, and in subsequent nestings the female often chooses a nest site near the boundary or actually outside the male's original territory. In these cases the male expands his territory to include the area around the new site. This causes many agonistic encounters including Fights. The most intense territorial encounters, which may continue almost uninterrupted for an hour or more, occur when two females build near a common boundary, or when a female tries to build within another's territory and not far from her nest. In some cases the intruder is able to gain part of the other's territory.

One female deserted a nest within the territory and selected another site about 60 meters (200 feet) from the old one and completely outside her territory. Her mate then attempted to establish a territory around her and the new nest site. In this case the male was able to gain only a very small area around the nest (about six square meters). He was probably unsuccessful because of the constant aggression of two other males that claimed parts of the area. The pair then left the area, and the female finally built a nest near the original territory.

Another pair was observed the morning following the destruction of their nest. The male exhibited a strong attachment to his territory around the old nest. However, the female did not come into this area, and explored an area completely outside his territory. The male exhibited ambivalent behavior (wing flicking and pivoting) indicative of low-intensity conflict situations. After several hours he left the old territory, moved into the area with the female, and began singing and defending the area.

Occasionally a pair disappeared. The cause of this is unknown. Then

TABLE 9
CONTEXT OF AGONISTIC BEHAVIOR PATTERNS

Behavior	*Boundary*	*Within territory (by owner male)*
Circling	frequent	rare
Chase	frequent	frequent
Titi	frequent	rare
Fights	frequent	rare
Chip	frequent	rare
Wings Out	rare	frequent
Muted Song	frequent	rare
Tail Spread	frequent	rare

there was a shift of the territory boundaries of several birds as each bird adjusted its boundaries somewhat and relinquished part of its old territory.

The initial stimulus for the establishment of the territory does not include the presence of the female, but after her arrival she is a stimulus for further territorial defense by the male. When a male had a choice between his old territory without the female and an unfamiliar area with the female, he chose the latter. Also, first-year males that fail to obtain mates cease defending an area after about two weeks. The male's attack tendency toward other males increases as soon as he has a female, as indicated by the inception of Fights and the longer duration of territorial encounters. A male will even cross a territorial boundary to follow his mate and will fight the owner male. Thus it seems that the female as well as the area may become the object of defense by the male.

Agonistic displays associated with territorial defense. During the breeding season the male is absolutely intolerant of other males on his territory. The agonistic behavior patterns that result depend on the position of the male in reference to his territory and the behavior of the other bird. Table 9 indicates the displays given by males at the boundary when there is a rival nearby and within the territory when another male intrudes.

Frequent displays and lengthy series of encounters are characteristic of the boundary zone. There are generally not many displays associated with the reaction of an owner to a rival in his territory. The owner simply chases him out, and if the rival does not leave, the owner may give Wings Out displays. Fights occur if the intruder's female is nearby and has invaded the territory.

It appears that those displays showing a conflict of attack and escape tendencies or a relatively stronger escape tendency are most prevalent at boundaries, while those indicating a stronger attack tendency are exhibited by the male within the territory, although there is some overlap.

The male reacts to an intruding female with several different behavior patterns, apparently depending on his stage in the reproductive cycle.

These include courtship, Chases, and Fights. At other times he merely ignores her. Thus there is no indication that he "recognizes" a strange female by reacting differently than he does to his own mate.

Female territorial behavior. The mates of the males involved in territorial encounters are usually present near the encounter. They generally do not become actively involved, but often give displays such as Tail Spread and Harsh Chips. On four occasions a female attacked a male as both males were resting between encounters. In two instances she attacked her own mate, and in the two other instances the other male. Apparently she does not recognize her own mate in such situations.

When a strange male approaches her, she usually gives Harsh Chips. Her mate then approaches and chases the intruder out of the territory. She never approaches or attacks the strange male herself, and there is no evidence that she recognizes the male as being a stranger since she also Chips when her own male approaches.

The female often attacks a female intruder, and Fights between females sometimes occur. On several instances prolonged encounters between females occurred, involving Circling, Fights, and Wings Out, typical of male territorial defense. Both males were usually present but did not participate.

Thus there is a division of labor between the sexes in territorial defense. This may be a reflection of the apparent lack of individual recognition of the mate in this species. Thus there would be selection against the male always reacting very aggressively toward females in the territory as he would probably treat his own mate in the same manner. The problem of keeping competing females out of the territory is thus solved by the female's aggression toward members of her own sex.

The principal role of the female in territorial defense involves the area immediately around the nest. Once a nest site is selected, the activities of the female are confined principally to this area, the male conducting most of his activities outside the area. The male seems less aggressive toward the female in this nest area, which includes an area of about six meters (20 feet) square, and rarely approaches her here. She usually threatens him unless he approaches in a courtship display. Thus the sexes are spatially isolated during late nest building and incubation, and aggressive encounters between the members of the pair are thereby reduced. Kendeigh (1952) states that the female seems to keep the male away from the nest in the following parulid species: Black-throated Green Warbler (*Dendroica virens*), Blackburnian Warbler (*D. fusca*), Magnolia Warbler (*D. magnolia*), and the Ovenbird (*Seiurus aurocapillus*).

The female reacts aggressively to the approach of certain other small species (other warblers, chickadees, vireos, etc.) in the nest area when

they approach to within nine meters (30 feet) of the nest. She flies directly at them, and the intruder usually leaves with no further encounters. If the other bird remains, the female usually approaches, Snarls, and sometimes Bill Snaps. Fights were recorded with a Red-eyed Vireo (*Vireo olivaceus*) and a Cerulean Warbler (*Dendroica cerulea*). In only one case was the male involved. This occurred when the female was away from the nest and a Baltimore Oriole (*Icterus galbula*) approached to within a few cm of the nest, and the male chased it off.

Species that approached the nest within nine meters and were usually ignored were the Wood Thrush (*Hylocichla mustelina*), Veery (*H. fuscescens*), and Catbird (*Dumetella carolinensis*), although in one instance the last species was attacked. A Wood Thrush nested only three meters (10 feet) away from a redstart, and it was never threatened or attacked although it was often perched near the redstart nest. Apparently the small species are attacked, while larger ones are usually ignored unless they approach the nest very closely. One of the functions of this nest defense is probably the prevention of damage to the nest by birds taking material.

The female reacts differently toward Brown-headed Cowbirds (*Molothrus ater*) than toward other species (Ficken, 1961). She threatens cowbirds even before she has selected a nest site, and during early nest building when she usually ignores other species. Cowbirds are also threatened at a greater distance from the nest than are other species.

Although females seem to exhibit territorial behavior with reference to the nest area, the displays utilized in its defense are not the same as those employed by the male in territorial defense, but rather are those generally associated with violations of individual distance. Females do possess displays similar to those used by males in territorial defense, but these are only employed against female conspecifics. Thus it would seem that the motivation of the female in defense of the nest area is different from that of the male in defending the territory as a whole.

Territorial behavior during the parental phase. While the female incubates, the male's movements are more restricted than earlier in the season, and he often sings for longer periods from a small area. Boundary conflicts are infrequent during the incubation period and become more so when there are young. Fights no longer occur, and even Circlings and Chases become rare. The territory boundaries are stable with none of the shifting noted in the nest-building period.

The young remain within the territory until they are independent and apparently migrate shortly afterward. The adults remain on the territory during the molt, although there is more wandering than formerly, and two males sometimes approach each other rather closely with no interaction. Thus the birds show some attachment to their territories even after their

aggressiveness decreases. Males show a slight increase in aggressiveness just prior to migration, and agonistic encounters sometimes occur between migrant males.

Some functions of territory in the redstart. The functions of territory in birds have been the subject of much discussion and have recently been reviewed by Carpenter (1958). Field observations of the redstart suggest some important implications of territoriality in this species.

In one case the nests of two pairs were very close, only about nine meters (30 feet) apart. For a few days one of the males courted the other's female more frequently than his own, although both females were in the same stage of the nesting cycle. Although the other male frequently chased him away, the intruding male did achieve copulation during the absence of the resident male. Although this is an unusual case, males from adjacent territories are attracted by the vocalizations of a soliciting female and sometimes copulate if the other male is not vigilant. The strong territorial defense exhibited by this species probably reduces the chances of copulation by other males.

Another possible function of territoriality in this species is the reduction of competition for nest sites. The redstart is not very specific regarding the height of the nest, or the species of plant involved, but there are rigid requirements for the spatial configuration of the branches, limiting the number of potential sites in the territory.

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SUMMARY

1. The agonistic displays of this species are described, and an attempt is made to analyze these in terms of causation, function, and derivation.

2. Most of the agonistic displays fall into two general categories: those concerned with the defense of individual distance and those concerned with territory. In many instances the displays given in the two contexts differ, but there is some overlap.

3. The male defends an area of about 0.3 hectares (0.75 acre) against intruding males, while the female defends the territory as a whole only against female conspecifics. In addition, the female reacts aggressively toward other small species in the nest area. She is also aggressive toward her mate, and there is a spatial isolation of the sexes during nest building

and incubation, since the female spends most of her time in the nest area.

4. There are many visual and vocal displays associated with territorial defense by males. Those displays that are confined to the boundary zone between adjacent territories are the ones that seem to reflect an attack-escape balance. On the other hand, males react with attack or with displays showing a strong attack tendency to the presence of intruders within the territory. Thus the reactions of the male are dependent both on position in relation to the territory and, to a lesser extent, on the reaction of the other male.

5. There are two main song types, apparently differing in motivation. The frequency of song types changes during the reproductive season, and the one that seems to express a weaker attack tendency becomes proportionately more common later in the season.

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