

COMPARATIVE ETHOLOGY OF THE CHESTNUT-SIDED WARBLER, YELLOW WARBLER, AND AMERICAN REDSTART

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COMPARATIVE studies are of great value in elucidating the evolution of behavior and one of the distinguishing characteristics of ethology is its emphasis on this approach (e.g. Lorenz, 1952; Tinbergen, 1959). Such research has added to our understanding of the evolution of avian communication systems, particularly displays. *Displays* have been 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." *Ritualization* is the process by which displays evolve from nonsignal precursors and usually includes the exaggeration of movements as well as changes in the readiness to respond to these movements so that they attain a communicatory function (Blest, 1961).

The criteria for homologies in behavior are the same as in morphology when there is no fossil record. Behavior patterns are probably of common origin when they are similar in form, widespread in a group, and have similar motivations, functions, and derivations (Tinbergen, 1959). We have capitalized names of behavior patterns which are probably displays and have given displays of different species the same name on the basis of Tinbergen's criteria.

The Wood Warblers (Parulidae) are particularly favorable subjects for comparative ethological studies because they are of relatively recent origin with many closely related species, have complex visual and vocal communication systems, and have undergone adaptive radiation into a variety of habitats with consequent behavioral changes (Ficken and Ficken, 1962). The purpose of this study is to describe and compare the reproductive behavior of several species of warblers, to indicate evolutionary trends in their displays, and finally to make some taxonomic comments.

METHODS

The American Redstart (*Setophaga ruticilla*) was studied intensively and since its behavior is described in detail elsewhere (Ficken, 1962, 1963), it will be referred to mainly for comparative purposes here. Almost all observations were made in an area of high population density in Ithaca, New York (Renwick Bird Sanctuary).

Chestnut-sided Warblers (*Dendroica pensylvanica*) were investigated on a brushy hillside along the railroad tracks in Varna, New York. The popula-

tion density was locally high, with the average territories of five adjacent males about 0.2 hectare in size. Observations were concentrated on these five birds during May, 1961, with subsequent more casual notations on other individuals. Watching took place before nest building was completed.

Yellow Warblers (*Dendroica petechia*) were studied principally at Howland's Island, New York, in May, 1962, and April and May, 1963. This was very favorable habitat with many 0.1-hectare territories; competition for them was intense (Ficken and Ficken, 1965). Approximately 10 pairs were studied during the period before the completion of nest building.

In addition, we observed some behavior patterns in other species of *Dendroica* on migration and, in the case of the Myrtle Warbler (*D. coronata*), in captivity. The Black-throated Green Warbler (*D. virens*) was observed during June, 1964 on Hog Island, Lincoln Co., Maine.

Notes on all species were spoken into a small portable tape recorder.

AGONISTIC BEHAVIOR

In all three species, most males arrive a few days before the females and immediately establish territories. During the first few days there are many conflicts within zones along territorial borders. Chestnut-sided Warblers however, have *fewer actual encounters* than in the other two species, even when the males are close together in the boundary zone. They may even feed about 10 feet apart in between boundary encounters; this never occurred in the other two species. However, Chestnut-sided Warblers tend to have prolonged disputes which involve intermittent encounters in the same location over several hours. Redstarts, and, to a lesser degree, Yellow Warblers, usually have *many encounters in a short time*, after which one or both males retreat well into their territories.

The following activities occur during or following male territorial encounters:

Circling.—This display occurs in several *Dendroica*. It is apparently confined to the boundary zone, and consists of a flight toward the opponent, then a turning away before reaching him. In the Chestnut-sided Warbler it is the *least ritualized*, often a simple arc made only in the general direction of the opponent but not reaching him closely or oriented at him. There is almost never any modification of wing beats or any response from the opponent. Yellow Warblers exhibit this display in the *least stereotyped* form, from a mere unoriented arc like that of the Chestnut-sided Warbler to nearly complete circles. At times a male Circles directly at the opponent, but often he does not. Occasionally the opponent Circles in response. Black-throated Green Warblers perform very circular flights, orienting toward an opponent and returning to near the original perch. Circling is most ritualized and least

TABLE 1
COMPARISON OF FREQUENCY AND FORM OF CIRCLING DISPLAYS IN FOUR SPECIES
OF WARBLERS

	Yellow	Chestnut-sided	Black-throated Green	Redstart
Frequency of display	++	+	++	++
Circularity	++	+	+++	+++
Stiff flight toward opponent	0	0	?	+++
Glide away from opponent	+	+	?	++
Approach closely to opponent	+	+	++	+++
Opponent responds by circling	+	0	++	+++
Oriented at opponent	++	+	+++	+++

? = not observed, 0 = apparently absent, + = rare, ++ = fairly common, +++ = frequent.

variable in the redstart; there is often a nearly perfect circle and the wing beats are usually modified (See Ficken, 1962; 608-609). The high degree of ritualization in the redstart, and the preceding species, is demonstrated by its signal value; the opponent usually Circling in return. Kendeigh (1945) reports Circling in the Magnolia Warbler (*D. magnolia*) although it is not as exaggerated as in the redstart. We did not observe this display in 3 years of intensive study of Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) and, except for the redstart, Circling has so far only been reported in *Dendroica*.

There is a graded series in the complexity of this display (Table 1). The condition in the Chestnut-sided Warbler is probably close to the primitive one. In fact, the lack of exaggeration of form and absence of an immediate response by the opponent indicate it may not be ritualized. This is also supported by its being given less frequently than in the other species. The redstart presents the advanced condition in this display in having great stereotypy and a well-defined signal function. This display probably functions as a threat (Ficken, 1962; Ficken and Ficken, 1965). It evidently expresses an attack-escape conflict in all species (Ficken, 1962).

Gliding.—This is a coasting flight with wing and tail spread wide, usually away from the opponent. Gliding is rare or fairly common in all three species during territorial encounters. It is most easily noticed in redstarts because their red wing and tail patches are maximally exposed.

Fighting.—Fighting is more ritualized in the redstart than in the other two. In fact, in this species it is often a "sham" and the birds do not strike each other. In the Yellow and Chestnut-sided Warblers the birds seem to hit each other and sometimes lock together.

Chases.—In the Chestnut-sided Warbler chases are simple and direct, while those of the redstart and Yellow Warbler are often more prolonged with many intricate turns.

Following occurs *only* in the Chestnut-sided Warbler. Unlike a chase in which the pursuer usually initiated the action, the opponent is simply followed as it flies away.

Supplanting was seen also only in the Chestnut-sided Warbler. The bird simply flies toward its opponent which then leaves and the first bird lands near where the second was perched.

Tail Spreading.—A frequent display in the redstart, it was observed several times after encounters in the Yellow Warbler and not at all in the Chestnut-sided.

Wings Out.—This posture in which the wings are held out from the body occurs in all three species after prolonged encounters. It is oriented at the opponent who usually retreats.

Moth Flight.—This display, in which the wings are beaten very rapidly and flight is slow, occurred only in the Yellow Warbler as a not infrequent part of agonistic encounters between males.

Sleeked Postures.—Preceding or, more commonly, following agonistic encounters, male redstarts often compress their feathers, giving them a very slim appearance. This is less frequent in the Yellow Warbler and was not observed at all in the Chestnut-sided Warbler.

The relative frequency of various nonvocal agonistic activities by unmated males is shown in Table 2 and other displays for which quantitative data are lacking are roughly graded according to frequency in Table 3. Fighting is about equally common in the three species. The Yellow Warbler and redstart are almost identical in the percentage of all agonistic activities. However, the Chestnut-sided Warbler differs in performing Circling less frequently and in Following and Supplanting the opponent. Many of the redstart displays reflect an attack–escape conflict (e.g., Circling, Gliding, Tail Spreading, and even Fighting). Behavior indicative of relatively strong escape tendency (e.g., Sleeked Postures) is also more common in this species. In addition, its tendency to attack an opponent also seems higher than in the other two species. Thus, the redstart expresses the *strongest attack* and *escape tendencies*, as well as the greatest conflict between these tendencies. The redstart also shows the *highest degree of ritualization of agonistic displays*. Circling is more exaggerated and has a greater signal value. Even Fighting appears ritualized. The Chestnut-sided Warbler, on the other hand, has less ritualized agonistic behavior and shows little evidence of an intense attack–escape conflict. This pattern is to be expected since displays usually express a conflict of two or more tendencies. The Yellow Warbler is intermediate in many respects.

TABLE 2
FREQUENCY OF NONVOCAL AGONISTIC BEHAVIOR OF UNMATED MALES DURING
TERRITORIAL ENCOUNTERS (EXPRESSED AS PER CENT OF TOTAL)

Activity	Species		
	Yellow (n = 49)	Chestnut-sided (n = 35)	Redstart (n = 55)
Fighting	24	27	23
Chases	42	21	40
Following	0	9	0
Supplanting	0	27	0
Circling	33	16	37

These species-typical differences in agonistic motivations are probably a reflection of historical differences in population density. Our observations on all three species were made in areas of locally high population density. However, the Chestnut-sided Warbler, which is dependent on clearings, was apparently very rare until recently (Bent, 1953), the Yellow Warbler was probably more confined to riverbanks than it is now, while the American Redstart has probably been very common for a longer time since it occupies the forest understory. There seems to be an increase in the development of agonistic signals in these species related to the number of conspecifics against which they once had to defend territories. Chestnut-sided Warblers presumably had few conspecifics nearby. The Yellow Warbler in a riparian environment probably had males on either side. The American Redstart, on the otherhand, had three or four adjacent conspecific males. The Chestnut-sided Warbler, and probably to a lesser degree the Yellow Warbler, have increased greatly in the last century as suitable habitat became abundant. However, the territorial displays which would seemingly be useful in populations with high densities have lagged behind.

Vocalizations.—These species have a variety of vocalizations which are

TABLE 3
OCCURRENCE OF AGONISTIC DISPLAYS IN THREE WARBLER SPECIES

Activity	Yellow	Species Chestnut-sided	Redstart
Sleeked Posture	+	0	+++
Wings Out	+	+	+
Gliding	+	+	+
Tail Spreading	+	0	+++
Moth Flight	++	0	0

0 = apparently absent, + = rare, ++ = fairly common, +++ = frequent.

TABLE 4
 CONTEXTS OF UNACCENTED ENDING SONGS (UES), ACCENTED ENDING SONGS (AES), AND MUTED SONGS (MUES, MAES)
 (EXPRESSED AS PERCENTAGE OF TOTAL SONG FOR THAT CONTEXT)

SPECIES	CONTEXT															
	Before arrival of females			Undisturbed on territory, pair formation through early nest building			Undisturbed on territory, late nest building			Following territorial encounters at boundaries						
	AES	MAES	MUES	AES	MAES	UES	MUES	AES	MAES	UES	MUES	AES	MAES	UES	MUES	
Chestnut-sided Warbler	95	0	5	0	91	0	9	0	24	0	24	51	3	0	83	14
			<i>n</i> = 40			<i>n</i> = 69				<i>n</i> = 41				<i>n</i> = 29		
Yellow Warbler	96	0	4	0	95	0	5	0	58	0	39	3	4	13	26	56
			<i>n</i> = 82			<i>n</i> = 42				<i>n</i> = 33				<i>n</i> = 46		
American Redstart	95	0	5	0	59	0	41	0	50	0	50	0	0	0	42	58
			<i>n</i> = 102			<i>n</i> = 22				<i>n</i> = 50				<i>n</i> = 32		

similar in form and context (Ficken and Ficken, 1962). Zeeps are commonly given during or preceding flight. Chips of two types occur in a variety of agonistic situations; these calls, harsh and metallic, at times grade into each other. Titis are rarer, occurring after prolonged territorial encounters. Females of some species of *Dendroica* as well as *Setophaga ruticilla* Snarl when the male approaches but this was not recorded in the Yellow or Chestnut-sided Warblers, perhaps because of insufficient observations. Bill Snaps frequently occur during or just preceding an attack in many warbler species. The above are the principal "call notes" of these species although there are some soft vocalizations which are infrequently heard and difficult to describe, such as the female Soliciting vocalization, certain calls between male and female at the nest, and notes of the young.

Song.—Each species has two principal song types, one with an accented ending (Accented Ending Song) and the other without this ending (Unaccented Ending Song) (Ficken and Ficken, 1962; 112–113). The types are well-defined in the restart but the Yellow and Chestnut-sided Warblers have some intermediates with a weak ending. The contexts of these songs in the three species are shown in Table 4.

Before the arrival of females over 90 per cent of the songs of these species have Accented Endings. However, in the American Redstart Unaccented Ending Songs become about equally common with Accented Ending Songs when nest building commences, and the same shift seems to occur slightly later (during egg laying and incubation) in the other two species. By the time of hatching, Unaccented Ending Songs predominate in all three species. In addition to this seasonal change in song type there is a difference in context earlier in the season. Songs immediately following territorial encounters are more frequently Unaccented Ending Songs and muted songs. The song types following encounters vary slightly according to the species. For example, the Yellow Warbler differs from the other two in singing Muted Accented Ending Songs as well as Muted Unaccented Ending Songs under these conditions.

We have attempted to determine the motivation of these songs from their contexts. Most encounters at boundaries end in a "draw," both birds retreating from the encounter area. More rarely, there are encounters within a male's territory and the territorial male is usually the victor, i.e., the other immediately retreats. Following such encounters the victorious male in all three species gives Accented Ending Songs more commonly and the vanquished male, Unaccented Ending Songs. The vanquished male presumably has a higher escape tendency (he fled from his opponent), indicating that the Unaccented Ending Song is more closely associated with escape. Sequences of songs by a single bird following boundary encounters give additional motivational cues. An example from our field notes involves an

unmated male redstart singing all Accented Ending Songs for an hour on his territory. Then he had an encounter with another male on a boundary after which he returned to his territory. He then sang five Muted Unaccented Ending Songs, and a minute later, all Unaccented Ending Songs. Three minutes after the encounter he alternated Accented Ending and Unaccented Ending Songs. Finally, 5 minutes after the encounter he sang all Accented Ending Songs. This example shows again that when the escape tendency is strong (although both attack and escape are presumably involved during territory encounters, escape is probably stronger immediately afterwards) Unaccented Ending Songs are more common. Additional evidence for the motivation of this song is that as aggressive and sexual tendencies decrease seasonally, and escape is thus relatively stronger, songs shift to the Unaccented type.

Sexual tendencies inhibit the territorial song, since males rarely sing near the female, particularly during courtship. Apparently the typical territorial song, the Accented Ending Song, occurs when there are no specific stimuli releasing strong aggression, escape, or sex. If sex or aggression is particularly strong, the birds are usually silent. If the escape tendency is high, they sing Unaccented Ending Songs or mute their songs.

Evidence for the function of these songs is more difficult to obtain. However, we do have some observational evidence that the Accented Ending Song is more attractive to conspecific females than the other song. In all cases we studied birds on adjacent territories which were similar in size and vegetational composition, in order to minimize these influences on the female's selection of a mate. One year we studied five unmated Chestnut-sided males on adjacent territories. Four sang all Accented Ending Songs, as would be expected at this time but the fifth was unusual in that he sang only Unaccented Ending Songs from the time of his arrival. This bird was the only one that failed to obtain a mate. In addition he was less successful in defending his territory boundaries against intrusions by other males. In another case a male redstart sang only Unaccented Ending Songs. When compared to five males on adjacent territories he was the last to obtain a female. Also, when compared to 15 other males he was the least aggressive and was unusual in that he tolerated the advances of other males into his territory. These observations suggest that Accented Ending Songs are more attractive to females than Unaccented Ending Songs and support further their motivational basis.

Related to its function in attracting a female, Accented Ending Songs seem to function in maintaining reproductive isolation. They are more species typical than the Unaccented Ending Songs which are sung more frequently after pair formation. Another bit of evidence of this function is that West Indian Yellow Warblers with fewer sympatric congeners, have songs that "resemble the more nondescript ones of North American forms but are oc-

asionally more melodious" (Bond in Griscom and Sprunt, 1957; 264). In Puerto Rico the resident Yellow Warblers sing only the Unaccented Ending Song (Francis G. Scheider, pers. comm.). This is also true in Cozumel, Yucatan, and Costa Rica, where this song is also more variable than in the north-eastern United States (Douglass Morse, pers. comm.).

A study of these songs gives additional evolutionary insights. The context in which Accented Ending Songs are given is slightly different in the three species studied, probably reflecting slight threshold differences, a common evolutionary trend. Threshold differences usually precede grosser changes in the form of a display and are often one of the first steps in the divergence of a display in closely related species (Hinde, 1959). The Unaccented Ending Song is probably the more primitive one since it is similar in several *Dendroica* species (Ficken and Ficken, 1962; 112).

COURTSHIP

Relations between members of a pair were studied intensively only in the redstart (Ficken, 1963), but the general pattern of sexual activity seems similar in the Chestnut-sided and Yellow Warblers. The male is initially aggressive toward the female. His aggression decreases gradually and his sexual tendency increases during nest building. Various displays are given during nest building and the day or two after the nest is completed. Copulation, at least in the redstart, occurs a day or two before the first egg is laid and then courtship activities cease.

Female courtship displays.—The female Soliciting posture is similar in many passerines, consisting of crouched body, vibrating wings, and often a low volume vocalization. Soliciting is similar in the redstart and Yellow Warblers, but was not observed in the Chestnut-sided Warbler. Females of all three species give Chips and Zeeps (Ficken, 1963) which probably keep the male aware of the female's presence and location.

Male courtship displays.—In the redstart male courtship displays are highly variable, including a varied combination of components (Ficken, 1963). Since only a few instances of courtship displays were recorded for the other two species, there is by no means a complete inventory.

Male redstarts and Chestnut-sided Warblers frequently Glide when flying away from the female. Moth flight occurs in the same context in the Yellow Warbler.

Fluffed displays, in which the body plumage is fluffed and the rump feathers ruffled, occur during early nest building in the Chestnut-sided Warbler and the redstart and are apparently identical. There were fewer observations of Yellow Warblers during this period and this display was not observed. Certain courtship displays occurring during late nest building, and apparently

reflecting an increased sexual tendency, were similar in the three species. The male approached the female within a foot with his wings extended horizontally. In the redstart the feathers were also fluffed. Kendeigh (1945) describes a slightly different version in the Chestnut-sided Warbler in which "The tail feathers are spread, the wings extended, and the crown feathers erected. The wings and tail quiver up and down."

Courtship displays of other species of *Dendroica* also include fluffing the plumage (including crown raising) and moving the wings in various ways (extending, spreading, vibrating) (Ficken and Ficken, 1962; 115). Although courtship displays are often divergent in closely related species (Hinde, 1959), distinctiveness is probably achieved in this group of closely related species by the differences in color and pattern exhibited by the displays. Another reason that these courtship displays do not show greater specific distinctiveness (Marler, 1957) is that they are not involved in pair formation. Therefore, other displays, primarily song, have greater specific distinctiveness in this group.

TAXONOMIC CONCLUSIONS

The redstart is remarkably similar in behavior to members of the genus *Dendroica*. In some cases the difference between the agonistic behavior of *D. petechia* and *D. pensylvanica* are greater than those between *D. petechia* and *Setophaga ruticilla*. A comparison of the behavior patterns of several *Dendroica* species (some species were observed for only a short time and only a few activities were noted), *Setophaga ruticilla*, and two *Vermivora* species is given in Table 5. The redstart shares 14 displays with *Dendroica* but only four of these with *V. chrysoptera* and *V. pinus*. Many of these shared behavior patterns are evolutionarily improbable (e.g., the possession of two song types differing primarily in the ending and occurring in similar contexts). This, combined with the number of shared displays, makes close relationship of the species involved highly probable.

Male redstarts do not attain fully adult breeding plumage until their second year, differing in this respect from other members of the family except the Olive Warbler, *Peucedramus taeniatus* (Webster, 1958). However, closely related species of other groups, e.g., Orchard and Baltimore Orioles (*Icterus spurius* and *I. galbula*) differ from each other in this respect and therefore, it does not seem a valid basis for generic separation of the redstart and *Dendroica*.

The genus *Setophaga*, including only the American Redstart (*S. ruticilla*) and the Painted Redstart (*S. picta*), was characterized by Ridgway (1902) on the basis of features such as the shape of the bill and the condition of the rictal bristles. Such characters were given great weight in the classical tax-

TABLE 5
COMPARISON OF BEHAVIOR OF WARBLERS OF DIFFERENT GENERA

Activity	<i>Dendroica</i> ¹	<i>Setophaga ruticilla</i>	<i>Vermivora chyroptera and V. pinus</i> ²
Vocal			
Harsh and Metallic Chips	×	×	0
Zeep	×	×	0
Titis	×	×	0
Snarl	×	×	0
Bill Snap	×	×	×
Unaccented Ending and Accented Ending Song ..	×	×	0
Nonvocal Agonistic			
Tail Spreading	×	×	×
Wings Out	×	×	0
Circling	×	×	0
Head Forward with Gape	×	×	×
Gliding	×	×	0
Moth Flight	×	0	×
Courtship			
Fluffed display	×	×	0
Male display with wings extended	×	×	0
Female Soliciting with vocalization	×	×	0

× = present (in the case of *Dendroica* in at least some species.
0 = not observed and apparently absent.

¹ Species studied include *D. petechia*, *D. pensylvanica*, *D. virens*, *D. magnolia*, *D. coronata*, *D. cerulea*, *D. fusca*.

² Ficken and Ficken, M.S.

onomy of the warblers. However, Parkes (1961) presented morphological evidence for the relationship of *S. ruticilla* to *Dendroica* and pointed out that the similarity of *S. picta* and *S. ruticilla* is probably the result of similar feeding habits and not indicative of close relationship. He concluded that *S. ruticilla* should be in a monotypic genus but placed near *Dendroica*. On the other hand *S. picta* shows affinities with the Central American redstarts of the genus *Myioborus* (Parkes, 1961; Ficken, 1965). More recently Phillips, Marshall, and Monson (1964) suggested that both *S. ruticilla* and *S. picta* should be included in the same genus as *Myioborus*. However, they apparently agree with Parkes and state that *S. ruticilla* has a “*Dendroica*-like song, eggs and tree nesting” and is therefore an “odd ball” in their proposed classification. The logic for their proposal is that “within *Dendroica* there is much diversity, and perhaps some should be allowed in *Setophaga* unless we are to ‘split.’” We think that both “splitting” and “lumping” are called for and that *Setophaga ruticilla* and *Dendroica* should be combined in the same genus and *S. picta* placed with *Myioborus*.

SUMMARY

The agonistic displays of the three species are described and related to differences in motivation which probably evolved through different selective pressures resulting from different historical population densities. The motivation, function, and evolution of song in this group are discussed. The species share similar song types, call notes, courtship, and agonistic displays. It is concluded that *Setophaga ruticilla* and *Dendroica* should be placed in the same genus.

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NEW LIFE MEMBER

Judith (Mrs. Bernard) Lewin, of Cote St. Loc, Montreal, Quebec has recently become a Life Member of the Wilson Ornithological Society. A housewife and mother of a small daughter, Mrs. Lewin finds time to devote to the study of local birds. Among her other interests is sculpture, and she would like to combine the two by doing bird sculpture. She and her husband have also been interested in bird photography. Besides the Wilson Society, Mrs. Lewin is a member of the Canadian Audubon Society, The Massachusetts Audubon Society, the Ontario Federation of Naturalists, and The Province of Quebec Society for Protection of Birds.

