

RESPONSES OF FOUR WARBLER SPECIES TO PLAYBACK OF THEIR TWO SONG TYPES

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RECENTLY renewed attention has been focused on the communicatory function of avian vocalizations (e.g. Marler, 1967; Smith, 1966). One problem in avian communication studies is determining what the message of a vocalization is for the recipient. The purpose of this study was to use song playback experiments to determine if intraspecific song variants have different messages. Few studies of the role of song have been made in species where each individual has more than one song type, although Hinde (1958) studied vocal responses of Chaffinches (*Fringilla coelebs*) to their two song types in captivity.

Many species of warblers have two song types that apparently differ in motivation and function (Ficken and Ficken, 1962, 1965; Morse, 1966, 1967). The American Redstart (*Setophaga ruticilla*), Chestnut-sided Warbler (*Dendroica pensylvanica*), and Yellow Warbler (*D. petechia*) possess an accented ending song (AE) and an unaccented ending song (UE). The Yellow Warbler also sings intermediate songs (IE) (Morse, 1966). In all three species song type AE is given more commonly by undisturbed, unmated males, while type UE songs are more common after pairing and during territorial encounters (Ficken and Ficken, 1965). The Black-throated Green Warbler (*D. virens*) has two song types, referred to as A and B by Morse (1967).

METHODS AND MATERIALS

All experiments were conducted near Damariscotta, Lincoln County, Maine, between 07:30 and 11:00 e.d.t. The first set of redstart experiments was conducted from 1-7 June 1966 and the second set 8-18 July 1966. Experiments with Black-throated Green Warblers were done 8-17 June 1966 and those with Chestnut-sided Warblers 30 June to 5 July 1966. Yellow Warbler experiments were conducted 31 May to 6 June 1967. The exact stage of the nesting cycle of the experimental birds was not determined, but on the basis of scattered observations, probably most Yellow Warblers and Black-throated Green Warblers were in the incubation period. Chestnut-sided Warblers probably had young during our playback experiments. Redstarts were probably incubating in the first experimental period and raising young in the later test period. First-year male redstarts are distinguishable from older males by plumage (Ficken and Ficken, 1967), but young and old males of the other three species cannot be told apart.

The location of experimental males was noted and in experiments with Chestnut-sided Warblers, Yellow Warblers, and Black-throated Green Warblers all were different individuals. Some of the redstarts studied late in the season were probably the same individuals that had been tested earlier, but at least 6 out of the 14 males in the second set were different individuals.

TABLE 1
 APPROACH RESPONSES OF AMERICAN REDSTARTS TO THEIR TWO SONG TYPES

| Individual no. | Playback of unaccented ending song | | Playback of accented ending song | |
|-------------------------------------|------------------------------------|----------------------------------|----------------------------------|-------------------------------|
| | No. of playbacks 10-30' of speaker | No. of playbacks <10' of speaker | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker |
| First-year males | | | | |
| 1 | 0 | 0 | 14 | 7 |
| 2 | 0 | 0 | 4 | 0 |
| 3 | 0 | 0 | 1 | 15 |
| 4 | 0 | 0 | 18 | 17 |
| 5 | 0 | 0 | 0 | 6 |
| Older males, early in season | | | | |
| 6 | 0 | 0 | 1 | 12 |
| 7 | 0 | 0 | 1 | 15 |
| 8 | 32 | 0 | 26 | 0 |
| 9 | 0 | 0 | 0 | 5 |
| 10 | 0 | 0 | 9 | 7 |
| 11 | 0 | 1 | 26 | 6 |
| 12 | 0 | 0 | 12 | 18 |
| 13 | 5 | 12 | 6 | 28 |
| 14 | 21 | 5 | 8 | 7 |
| 15 | 25 | 6 | 0 | 0 |
| 16 | 0 | 0 | 16 | 11 |
| 17 | 21 | 9 | 12 | 15 |
| Older males, later in season | | | | |
| 18 | 12 | 0 | 0 | 0 |
| 19 | 10 | 0 | 17 | 0 |
| 20 | 10 | 13 | 12 | 8 |
| 21 | 8 | 0 | 16 | 10 |
| 22 | 18 | 0 | 19 | 16 |
| 23 | 7 | 21 | 23 | 10 |
| 24 | 0 | 0 | 1 | 9 |
| 25 | 19 | 7 | 14 | 22 |
| 26 | 20 | 0 | 0 | 22 |
| 27 | 0 | 0 | 3 | 0 |
| 28 | 3 | 2 | 2 | 14 |
| 29 | 0 | 0 | 12 | 16 |
| 30 | 0 | 0 | 26 | 4 |

Males were selected for experiments if they sang consistently during a 6-minute initial baseline regardless of whether they sang during later baselines. The experimental procedure was similar to that used by Milligan (1966). In experiments with Chestnut-sided Warblers and American Redstarts UE songs of the species being studied were played following the initial baseline. A second 6-minute baseline was taken and then AE songs were played. A final 6-minute baseline followed. UE was played first to these two species because our hypothesis was the UE would be responded to more weakly than AE, and it seemed desirable to present the weaker of the two stimuli initially to minimize "carry over." Table 1 indicates that redstarts responding to UE showed no apparent difference in response to AE compared to those that did

not respond to UE. The results of all experiments indicate that "carry over" from one playback to the next as measured by approaches seems minimal.

We had no prior indication as to which of the Black-throated Green Warbler and Yellow Warbler songs would evoke the strongest responses. In the first eight experiments with Black-throated Green Warblers we played song type A first, in the second eight experiments song type B. In Yellow Warbler experiments we played song IE first in eight experiments and AE first in six.

During all playbacks we played 36 songs at 10-second intervals, i.e. from the beginning of one song to the beginning of the next.

During both baseline and playback periods we noted the number and type of all songs sung, also the positions of males in reference to the speaker. The baseline periods, during which no songs were played, served as controls. Stimulus songs of Chestnut-sided Warblers were from our own field recordings of two different individuals in Maine. Recordings of the other species, in each case a different individual, we obtained from the Federation of Ontario Naturalists warbler record.

Figure 1 shows spectrographs of stimulus songs used in these experiments. The two Yellow Warbler songs used for playback are very similar except that the IE has only part of the ending found in AE. In the other species the AE- and UE-type songs are quite different, as are the A- and B-type songs of the Black-throated Green Warbler.

We used a Uher 4000 S portable tape recorder and a Nagra DH amplifier-speaker, and played tapes at 7.5 i.p.s. The speaker was placed at least 50 feet away from the singing males at the onset of experiments, and observers remained at least 20 feet from the speaker.

RESULTS

Responses of American Redstarts.—We noted the number of playback songs during which males were between 10 and 30 feet of the speaker and closer than 10 feet to the speaker (this last category also included some flights over the speaker). Table 1 summarizes our findings on these measures of responsiveness to both song types in the American Redstart.

Unfortunately, our sample size of first-year males was small. All five first-year males reacted to song type AE but none to UE. First-year males showed no significant difference from older males in the number of playbacks in which they approached the speaker closer than 10 feet when song type AE was played ($P > 0.05$, using a Mann-Whitney U test).

Only 6 of 12 older males in the first set of experiments and 9 of 13 males in the later set approached the speaker to within 30 feet when UE was being played. Also, redstarts spent significantly more time within 10 feet of the speaker when AE was played than when UE was played ($P < 0.01$ using a Wilcoxon matched-pairs signed-ranks test).

Approaches closer than 10 feet to the two song types showed no differences between the early and later playback periods ($P > 0.02$ using a Mann-Whitney U test).

In trying to do playbacks during the later period finding singing males

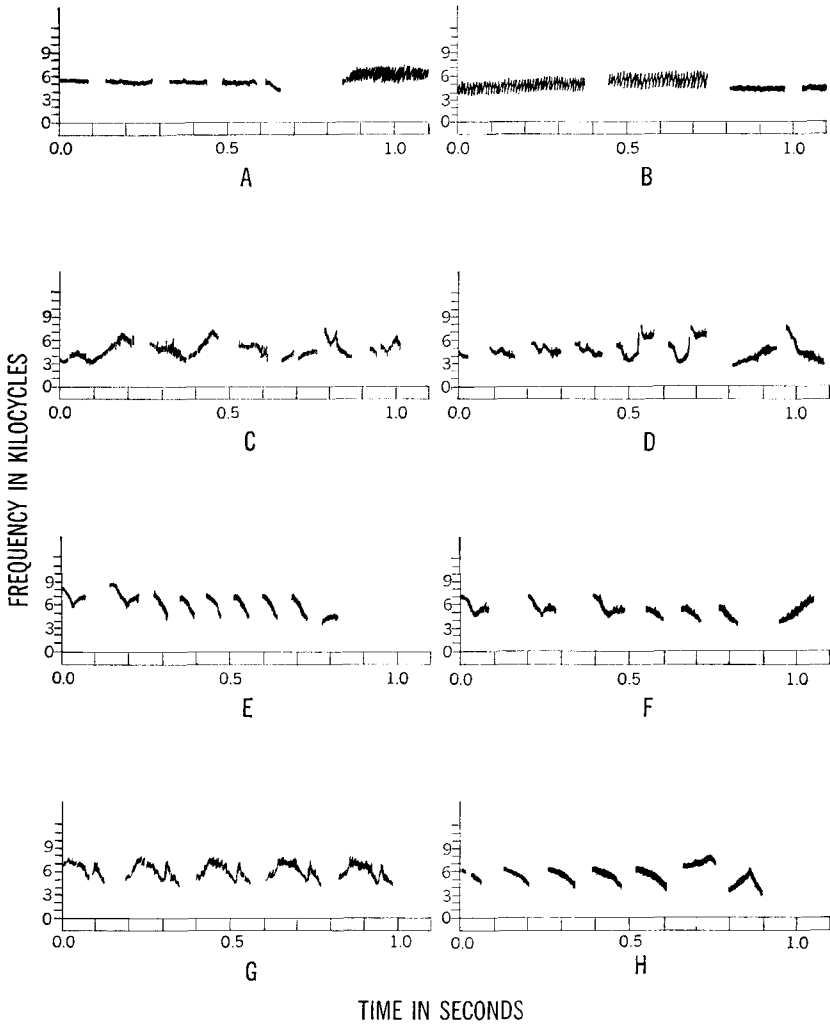


Figure 1. Sound spectrographs of warbler songs. A. Black-throated Green Warbler song B. Black-throated Green Warbler song A (last note omitted because of space but is the same as the second note). C. Chestnut-sided Warbler song AE. D. Chestnut-sided Warbler song AE. E. Yellow Warbler song IE. F. Yellow Warbler song AE (two introductory notes omitted that are the same as the first three notes shown). G. American Redstart UE. H. American Redstart AE.

was more difficult; there seemed to be a general decrease in singing. Those males that sang constantly for the 6-minute initial baseline showed a marked decrease in the number of songs per 6 minutes as com-

TABLE 2
COMPARISON OF NUMBER AND TYPE OF SONGS GIVEN BY MALE AMERICAN REDSTARTS
EARLY AND LATER IN THE SEASON DURING BASELINES

| | Songs | | Total |
|-------------------|------------------------|----------------------|-------|
| | Unaccented ending song | Accented ending song | |
| Early (n = 12) | 297 | 273 | 570 |
| Later (n = 13) | 154 | 212 | 366 |

pared to earlier periods ($P < 0.001$ using a Chi-square test). Furthermore, the proportion of AE type songs given during this period increased significantly in comparison to the earlier period ($P < 0.001$) (Table 2).

Table 3 shows the number and type of songs given in all redstart experiments during the first two baseline periods and the two playback periods. Playback of UE did not change the ratio of AE to UE ($P > 0.05$) and no significant difference existed in this ratio in the two baselines ($P > 0.05$). However, during playback of AE, AE increased significantly ($P < 0.05$). Muted (low volume) songs of both types occurred only during playback.

In four cases female redstarts responded to playback; the three that responded to type AE song come to within 30 feet of the speaker near the beginning of playback and chipped continuously. Their mates came in later, possibly drawn to the vicinity of the speaker by the females' chips, which have a strong attraction for males.

Responses of Chestnut-sided Warblers.—Table 4 compares responsiveness to Chestnut-sided Warbler UE and AE songs using the same mea-

TABLE 3
NUMBER AND TYPE OF SONGS IN BASELINES AS COMPARED TO SONGS DURING PLAYBACKS
IN AMERICAN REDSTARTS AND CHESTNUT-SIDED WARBLERS¹

| Species | Initial baseline | | | | Playback of UE | | | | Baseline | | | | Playback of AE | | | |
|------------------------|------------------|-----|-----|-----|----------------|-----|------------------|------------------|----------|-----|------------------|------------------|----------------|-----|------------------|------------------|
| | UE | AE | mUE | mAE | UE | AE | mUE ¹ | mAE ¹ | UE | AE | mUE ¹ | mAE ¹ | UE | AE | mUE ¹ | mAE ¹ |
| American Redstart | 486 | 673 | - | - | 252 | 440 | 47 | 40 | 302 | 507 | - | - | 154 | 358 | 130 | 65 |
| Chestnut-sided Warbler | 80 | 318 | - | - | 132 | 233 | 32 | 20 | 49 | 297 | - | - | 31 | 151 | 25 | 53 |

¹ m = muted, UE = unaccented ending song, AE = accented ending song.

TABLE 4
 APPROACH RESPONSES OF CHESTNUT-SIDED WARBLERS TO THEIR TWO SONG TYPES

| Individual no. | Playback of UE ¹ | | Playback of AE ¹ | |
|-------------------|------------------------------------------|----------------------------------------|------------------------------------------|----------------------------------------|
| | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker |
| 1 | 0 | 2 | 3 | 26 |
| 2 | 26 | 5 | 10 | 23 |
| 3 | 19 | 6 | 11 | 33 |
| 4 | 18 | 14 | 10 | 22 |
| 5 | 22 | 3 | 13 | 20 |
| 6 | 1 | 29 | 0 | 36 |
| 7 | 0 | 0 | 19 | 11 |
| 8 | 13 | 1 | 3 | 23 |
| 9 | 5 | 0 | 7 | 21 |
| 10 | 7 | 5 | 16 | 19 |
| 11 | 21 | 7 | 3 | 31 |
| 12 | 0 | 1 | 0 | 14 |
| 13 | 1 | 29 | 1 | 33 |

¹ AE = Accented ending song, UE = Unaccented ending song.

tures of approach as in the redstart experiments. Chestnut-sided Warblers also responded more strongly to AE than UE as measured by number of playbacks closer than 10 feet to the speaker ($P < 0.005$ using a Wilcoxon matched-pairs signed-ranks test).

The proportion of type AE and type UE songs did not differ in the two baseline periods ($P > 0.05$) (Table 3). During playback of UE the proportion of UE increased ($P < 0.001$). The ratio of AE to UE showed no significant difference between AE playback and the baseline period ($P > 0.05$). During playback of UE muted UE songs were more frequent, and during playback of AE muted AE were more frequent.

Responses of Black-throated Green Warblers.—Table 5 shows the approach responses to the two song types. Males responded more strongly to type A song as measured by the number of playbacks with approach to closer than 10 feet from the speaker whether type A song was first or last in the playback sequence ($P < 0.05$ using a Wilcoxon matched-pairs signed-ranks test).

The type of songs given during playback and baseline periods was also studied (Table 6). During the initial baseline preceding playback birds sang predominately type A songs. When A was played back first, no change was evident in the amount of song or in the type of songs ($P > 0.05$) during A playback. When type B was played first, subsequent playbacks of A produced a significant increase in type B songs ($P < 0.001$). In both sets of experiments the songs given during the first playback

TABLE 5
 APPROACH RESPONSES OF BLACK-THROATED GREEN WARBLERS TO PLAYBACK OF THEIR
 TWO SONG TYPES

| Individual no. | Playback of A song | | Playback of B song | |
|---------------------|------------------------------------------|----------------------------------------|------------------------------------------|----------------------------------------|
| | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker |
| A song played first | | | | |
| 1 | 5 | 27 | 24 | 0 |
| 2 | 15 | 4 | 10 | 16 |
| 3 | 0 | 27 | 25 | 0 |
| 4 | 13 | 16 | 22 | 2 |
| 5 | 0 | 28 | 7 | 27 |
| 6 | 9 | 25 | 12 | 3 |
| 7 | 20 | 6 | 6 | 2 |
| 8 | 12 | 16 | 19 | 4 |
| B song played first | | | | |
| 9 | 5 | 28 | 11 | 7 |
| 10 | 26 | 6 | 0 | 0 |
| 11 | 1 | 33 | 13 | 10 |
| 12 | 10 | 17 | 21 | 0 |
| 13 | 18 | 17 | 16 | 4 |
| 14 | 15 | 19 | 21 | 3 |
| 15 | 2 | 32 | 15 | 16 |
| 16 | 9 | 25 | 20 | 4 |

tended to carry over to the second playback. Although birds tend during playback to sing the same song being played to them, this was not true when the second playback was influenced by the first. Some muted songs (primarily A during playback of A and B during playback of B) were also heard.

Responses of Yellow Warblers.—No significant difference was evident between responses to AE and IE as measured by number of playbacks with approach closer than 10 feet to the speaker regardless of whether IE or AE was played first ($P > 0.05$, Table 7). The Yellow Warbler does not discriminate between these two songs as measured by approaches.

TABLE 6
 NUMBER AND TYPE OF SONGS IN THE INITIAL BASELINE AS COMPARED TO PLAYBACK TO
 BLACK-THROATED GREEN WARBLERS

| Experimental setup | Initial baseline | | Playback of A | | Playback of B | |
|-----------------------|---------------------|----|------------------|----|------------------|----|
| | A | B | A | B | A | B |
| A played first | 216 | 0 | 160 | 5 | 167 | 13 |
| B played first | 249 | 16 | 85 | 65 | 56 | 81 |

TABLE 7
 APPROACH RESPONSE OF YELLOW WARBLERS TO PLAYBACK OF TWO DIFFERENT SONGS

| Individual no. | Playback of IE ¹ song | | Playback of AE ¹ song | |
|----------------------|------------------------------------------|----------------------------------------|------------------------------------------|----------------------------------------|
| | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker | No. of playbacks 10-30' speaker | No. of playbacks <10' speaker |
| IE song played first | | | | |
| 1 | 9 | 18 | 2 | 31 |
| 2 | 0 | 34 | 3 | 32 |
| 3 | 12 | 13 | 8 | 11 |
| 4 | 11 | 18 | 4 | 17 |
| 5 | 12 | 10 | 10 | 10 |
| 6 | 14 | 21 | 10 | 26 |
| 7 | 15 | 18 | 26 | 10 |
| 8 | 23 | 10 | 27 | 1 |
| AE played first | | | | |
| 9 | 16 | 18 | 26 | 12 |
| 10 | 4 | 25 | 11 | 20 |
| 11 | 1 | 31 | 6 | 23 |
| 12 | 4 | 28 | 1 | 35 |
| 13 | 7 | 28 | 5 | 29 |
| 14 | 8 | 23 | 7 | 25 |

¹ IE = intermediate song, AE = accented ending song.

The songs given by Yellow Warblers were not analyzed because of the difficulty of describing intermediate songs.

DISCUSSION

Playback of different natural song types led to differential responsiveness in three species. Thus the song repertoire of these warblers contains at least two distinctive signals, probably having slightly different messages. To determine the message content of a signal is difficult, although as Marler (1967) suggests, comparing the experimental response with behavior in other situations for which the approximate motivation of the bird is known is a good guide. The flights over the speaker and other direct approaches to the sound source are similar to aggressive actions observed in natural territorial encounters. Therefore we conclude that AE songs of Chestnut-sided Warblers and American Redstarts stimulate more aggressive actions than UE songs and that type A song of the Black-throated Green Warbler stimulates more aggressive responses than song type B. The Yellow Warbler, which apparently has a graded song system, did not differentiate between two songs, one of which represented an intermediate condition.

Individual differences in responsiveness, particularly marked in redstarts, may be due to uncontrolled variables in our experiments such as

proximity to the nest, location of playback with respect to territorial boundaries, and differences in the precise stage of the nesting cycle.

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SUMMARY

Many species of warblers sing two different song types that apparently differ in motivation and function. Playback experiments were conducted in the field with American Redstarts, Chestnut-sided Warblers, Black-throated Green Warblers, and Yellow Warblers. The first three species responded differentially to playback of their two song types. Redstarts and Chestnut-sided Warblers responded by approaching more closely to accented ending songs (AE) than to unaccented ending songs (UE) and Black-throated Green Warblers reacted more strongly to type A song than to type B. Yellow Warblers, which apparently have a graded song signal, did not differentiate, either by approaching or by song changes between two very similar songs. Redstarts showed no age differences in response to AE and no difference in responsiveness between experiments done early and later in the season, although song decreased during the later period. During playback redstarts, Black-throated Green Warblers, and Chestnut-sided Warblers tended to sing relatively more songs of the type being played back.

LITERATURE CITED

- FICKEN, M. S., AND R. W. FICKEN. 1962. The comparative ethology of the wood warblers: a review. *Living Bird*, 1: 103-122.
- FICKEN, M. S., AND R. W. FICKEN. 1965. The comparative ethology of the Chestnut-sided Warbler, Yellow Warbler and American Redstart. *Wilson Bull.*, 77: 363-375.
- FICKEN, M. S., AND R. W. FICKEN. 1967. Age-specific differences in the breeding behavior and ecology of the American Redstart. *Wilson Bull.*, 79: 188-199.
- HINDE, R. A. 1958. Alternative motor patterns in Chaffinch song. *Anim. Behav.*, 6: 211-218.
- MARLER, P. 1967. Animal communication signals. *Science*, 157: 769-774.
- MILLIGAN, M. 1966. Vocal responses of White-crowned Sparrows to songs of their own and another species. *Anim. Behav.*, 14: 356-361.
- MORSE, D. H. 1966. The context of songs in the Yellow Warbler. *Wilson Bull.*, 78: 444-455.
- MORSE, D. H. 1967. The contexts of songs in Black-throated Green and Black-burnian Warblers. *Wilson Bull.*, 79: 64-74.
- SMITH, W. J. 1966. Communication and relationships in the genus *Tyrannus*. *Publ. Nuttall Ornithol. Club*, no. 6.

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