The Auk 111(3):730–734, 1994

Different Responses to Different Song Types in American Redstarts

DANIEL M. WEARY,[1] ROBERT E. LEMON, AND STEPHANE PERREAULT
Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, Quebec H3A 1B1, Canada

The idea that bird song has both intrasexual and intersexual functions is now firmly ingrained in the literature (see McGregor 1991). Evidence for the intrasexual function comes from an abundance of studies showing that territorial males respond aggressively when songs are played to them within their territories (reviewed by Falls 1992). Furthermore, we know that song is an effective territorial deterrent, as song played from vacant territories has been shown to reduce the speed of invasion by new birds (e.g. Krebs et al. 1978), and males that cannot sing are less able to maintain their territories (e.g. Peek 1972, MacDonald 1989). The intersexual function has also been convincingly demonstrated. For example, laboratory presentations of song to females often evoke a sexual solicitation display (reviewed by Searcy 1992), and females are attracted to nest boxes with loudspeakers playing song (Eriksson and Wallin 1986, Mountjoy and Lemon 1990).

Given that male songbirds direct song towards females and males, the question remains as to the relative importance of these different functions. When a male sings, is it doing so to attract mates or repel intruders? For birds that sing only a single song type, this question may be difficult to answer. Even in species in which each male sings more than one song type (i.e. a repertoire of songs), these songs may be functionally interchangeable. Certain species, such as those in the Parulinae, may be an exception as they divide the songs in their repertoire according to function (for review, see Spector 1992). The singing behavior of American Redstarts (*Setophaga ruticilla*) provides an example (see Lemon et al. 1987). In certain circumstances, male redstarts sing a single song type over and over ("repeat song"), but at other times they sing a repertoire of song types with little immediate repetition ("serial song"). Repeat song is more common when near the nest and early in the breeding season prior to the termination of egg laying by the female, whereas serial singing is more common at other times.

Several other species of warblers also have two song modes or types that appear to be homologous to the ones described for redstarts. Kroodsma et al. (1989) showed that Chestnut-sided Warblers (*Dendroica pensylvanica*) sing the equivalent of repeat songs early in the season and when unmated, whereas the equivalent of serial songs are used more during interactions with other males. Spector's (1991) observations indicate a similar pattern for Yellow Warblers (*D. petechia*). These studies also demonstrated that when a female is removed from a male's territory, the male's use of the repeat song equivalent increases. These observations suggest that repeat song types may have more of an intersexual function, whereas the serial song types have more of an intrasexual function.

If American Redstarts use their two song modes for these different functions, how might we expect territorial males to respond to playback of these different stimuli? The most straightforward prediction is that male response should be greatest to the supposedly male-directed serial song. To date, three studies have attempted to test this prediction, but each has produced a different result. Ficken and Ficken (1970) found that American Redstarts (as well as Chestnut-sided Warblers and Black-throated Green Warblers, *D. virens*) responded more to their equivalent of repeat song, MacNally and Lemon (1985) found that redstarts responded equally to the two modes, and Weary et al. (1992) found that redstarts responded more to serial songs.

The response of males to the two modes may vary over time. Both Ficken and Ficken (1970) and MacNally and Lemon (1985) argued that such a difference might occur because the birds' use of the two modes tends to vary over the course of the breeding season. There are also functional reasons for predicting a change. Playback of repeat songs should provoke some response because a competitor trying to attract females must be a threat to the territory holder, but this threat should decrease as the season progresses because cuckoldry becomes impossible once the entire clutch has been laid. Therefore, males should respond strongly to playback of both modes early in the breeding season, but once egg laying is complete, serial song should evoke stronger responses than repeat song.

There are two important differences between repeat and serial singing. In addition to the obvious difference in versatility (the repeat mode having one song sung repeatedly and serial songs being performed in a versatile sequence), different types of songs tend to be used in the different modes (Fig. 1). The song types used in the two modes tend to differ in a number of ways, but one of the most characteristic is the presence of terminal notes, called accents (Lemon et al. 1985). These accents are themselves known

[1] Present address: Center for Food and Animal Research, Building 94, Central Experimental Farm, Ottawa, Ontario K1A 0C6, Canada.

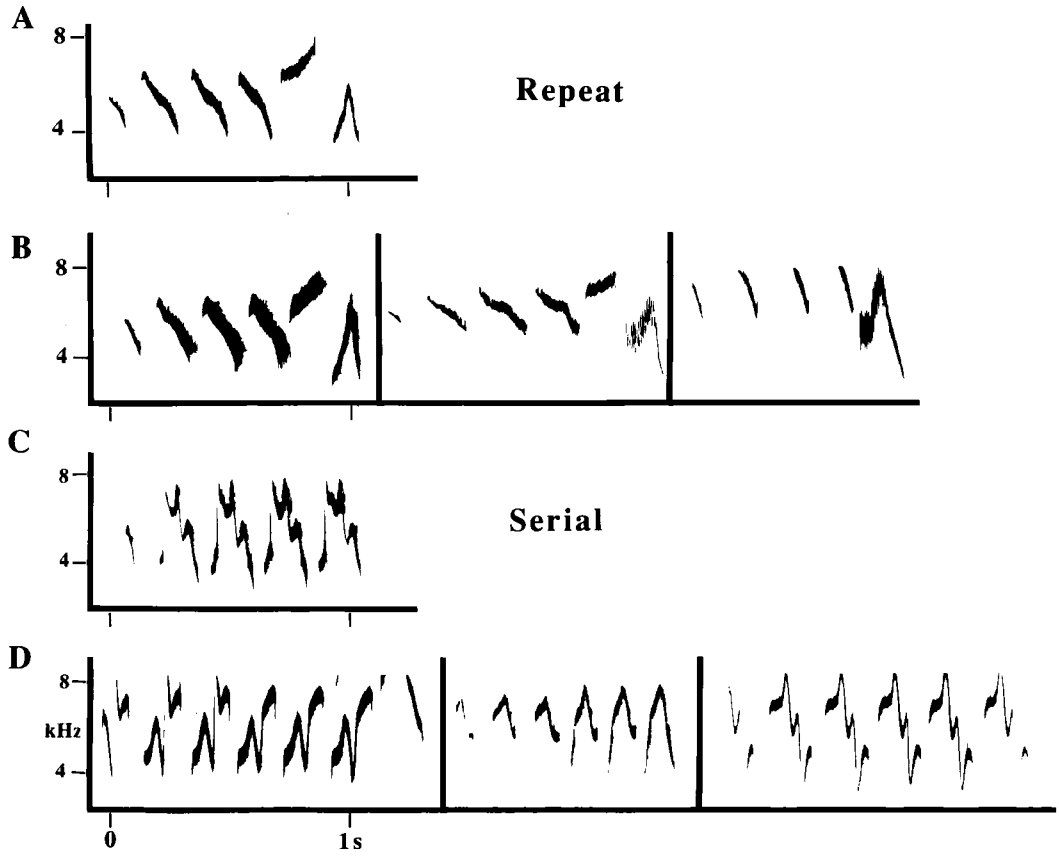

Fig. 1. Wide-band sonagrams of one set of song stimuli presented to subjects. All songs are of American Redstarts from St. Andrews, New Brunswick. Subjects were played: (A) repetitions of a single accented repeat song; (B) repetitions of a sequence of different accented repeat songs; (C) repetitions of a single unaccented serial song; and (D) repetitions of a sequence of different unaccented serial songs. Typical repeat mode singing was simulated by (A) and typical serial mode singing was simulated by (D).

to affect response (Date et al. 1991). Repeat song types normally possess these accents, but serial song types do not. Thus, the playback of one mode may evoke a stronger response than the other because of the difference in song types used or the difference in versatility.

We attempted to resolve the conflicting evidence concerning response to the two modes by performing a new experiment. We played sequences of repeat and serial songs to territorial male redstarts. We performed trials at three different times to determine whether the time of the breeding season affected response to the two modes. We independently varied song type and versatility in the playback tapes so that the nature of these two effects could also be determined.

Methods.—The experiment consisted of three sets of 24 trials (total of 72), all conducted during June 1991. The first set of trials took place from 3–9 June, the second from 11–16 June, and the third from 24–26 June. All trials were performed between 0600 and 1200, or 1800 and 2000 EST within 20 km of St. Andrews, New Brunswick, Canada. Subjects were not banded, so we ensured the use of a different subject in each of the 72 trials by moving a minimum of 100 m between trials. Our studies of banded individuals indicate that territories are usually less than one-half this diameter. The territorial boundaries of the subjects used in our study were not known, so in each trial we placed the playback speaker near the singing locations of the subject and away from its neighbors. The nesting stages of subjects were also not known, but our own work on known birds indicates that during the first set of trials subjects were likely to be at the egg-laying stage, during the second set females were likely to be incubating, and during the last set subjects were likely to be feeding young.

Songs were recorded at close range at a tape speed of 19 cm/s using a Uher 4000 recorder, and a Sennheiser MD211 microphone mounted in a Dan Gib-

son parabolic reflector. Recordings were made in 1989 in a part of our study area not used during this experiment, so it is likely that these songs were unfamiliar to all subjects. Eight different repeat songs were recorded from eight different males and eight different serial songs were recorded from eight other males. Songs were digitally spliced to form a sequence using SoundEdit software and a Macintosh computer, and then rerecorded at a rate of 10/min for 2 min to make playback tapes.

Four different playback tapes were necessary to test the effects of song type (accented vs. unaccented) and versatility (repeated vs. sequence): (1) repetitions of a single accented repeat song type (Fig. 1A); (2) repetitions of a single unaccented serial song type (Fig. 1C); (3) repetitions of a sequence of three different accented repeat song types (Fig. 1B); (4) repetitions of a sequence of three different unaccented serial song types (Fig. 1D). Within each set of 24 trials, the four tapes were played to each subject in a different, randomly assigned order. Two sets of the four different playback tapes were generated. Each subject was assigned randomly one set or the other, within the constraint that, for each set of 24 trials, 12 subjects were played one version and 12 subjects the other.

Playback was through a Marantz PMD 221 tape recorder attached to a Realistic Minimus 0.6 amplifier/loudspeaker placed 1.5 m off the ground. The amplitude at which each tape was played was standardized to peak at 100 dB at 0.5 m using a Radio Shack (42-3010) sound-pressure-level meter. Trials began with a 2-min prestimulus silent period. Then the four stimuli were presented for 2 min each, with 4 min of silence between them. While the songs were played (presentation period), and during the 2 min immediately following each presentation (after period), observers monitored two responses of the subject: minimum distance (m) of approach to playback speaker; and time (s) spent within a 7-m radius of speaker. These two response measures had proven to be powerful discriminators in a previous experiment employing a similar within-subject design (Weary et al. 1992).

Data were analyzed using a general linear model. The differences between the four stimuli were included as two within-subject effects in a repeated-measures analysis of variance. Changes in response among the three phases of the experiment were analyzed as an among-subject effect. Differences between the two versions of the playback stimuli were also incorporated as an among-subject effect, but neither this effect nor any of the interactions between it and the within-subject effects was significant.

Results.—Redstarts responded vigorously to both repeat (accented) and serial (unaccented) song types, either when a single song was repeated or when a sequence of different songs was played. When the three stages of the experiment were considered together, the birds did not respond significantly more to unaccented than to accented songs (time within 7 m, $F_{1,70} = 2.22$, $P > 0.1$; minimum distance, $F_{1,70} = 0.24$, $P > 0.3$), or more to versatile than to repetitive sequences (time within 7 m, $F_{1,70} = 0.01$, $P > 0.3$; minimum distance, $F_{1,70} = 0.97$, $P > 0.3$). Furthermore, the interaction between song type and versatility was not significant (time within 7 m, $F_{1,70} = 0.62$, $P > 0.3$; minimum distance, $F_{1,70} = 0.01$, $P > 0.3$).

We had predicted that response should be similar to playback of the two song modes early in the breeding season, but that later, when egg laying was complete, subjects should respond more strongly to the unaccented, serial sequences. To test for this possibility, we examined the interactions between this effect of experimental period and those of song type and versatility. We found a significant interaction between period and song type in terms of time spent within 7 m ($F_{1,70} = 4.83$, $P < 0.05$). No other interaction effect was significant ($P > 0.3$).

In order to determine the nature of the significant interaction between experimental period and song type, we divided the data into the three periods, each consisting of a repetition of 24 trials. We restricted this part of the analyses to one response measure, time within 7 m, because it was this variable that showed the significant interaction effect. During the last period (24–26 June), redstarts responded significantly more to unaccented songs than to accented songs ($F_{1,23} = 7.65$, $P < 0.015$). In the two earlier periods, this effect was not significant (3–9 June, $F_{1,23} = 1.60$, $P > 0.2$; 11–16 June, $F_{1,23} = 0.76$, $P > 0.3$). Neither the effect of versatility nor the interaction between song type and versatility was significant in any of the three periods.

Discussion.—As part of an experiment designed to test a different hypothesis, Weary et al. (1992) found that redstarts showed a stronger response to serial singing than to repeat singing. That experiment was conducted during the last week of June. The present study was designed to: (a) replicate this test; (b) determine how response to the two modes varies across the breeding season; and (c) determine whether song type or song versatility is the important factor. The subjects in the present experiment responded strongly to both modes, but during the latter part of the breeding season subjects showed a stronger response to serial songs. These findings seem consistent with the hypothesis that repeat songs have more of an intersexual function than serial songs, whereas serial songs have more of an intrasexual role. The seasonal effect that we found could have been due to any number of factors that changed over the three periods, but we suggest that one important element is the change in the reproductive status of the female.

The difference in response was due to the difference in the song types used rather than the difference in versatility. When repeat song types and serial song types (accented and unaccented songs) were presented in sequences of equivalent versatility, subjects

responded more to the serial song types. However, subjects did not distinguish between sequences of different versatility made up of the same song types. The fact that subjects responded to song type and not to versatility is intriguing because we define the two modes on the basis of the latter. There is other evidence that the song types used by American Redstarts are themselves biologically important. Males that use unaccented song types in their repeat singing tend to have higher seasonal reproductive success than males that use accented song types (Lemon et al. 1992).

The results from both this study and Weary et al. (1992) seem to contrast with those from MacNally and Lemon (1985), in which no difference in response to the two modes was detected. MacNally and Lemon performed their experiment at two times during the breeding season, but their "late season" period was from 13–17 June, a time when many redstarts in the study population are still laying. Thus, the results of MacNally and Lemon agree with our findings in that both fail to show a difference in response during mid-June.

One other study tested for a difference in response to repeat and serial songs in American Redstarts (and three other species of wood-warbler). Ficken and Ficken (1970) found that redstarts actually responded more strongly to repeat than to serial songs. They also tested birds twice during the breeding season, but both tests were after the end of egg laying. However, the significance of their results is difficult to judge for a number of reasons (see MacNally and Lemon 1985).

Several authors have argued that the two song modes used by warblers may signal different motivational states. The basic argument (Ficken 1962, Morse 1966, Lein 1972) is that repeat songs are given as the ambient or default song, during low intensity interaction, but serial songs are used in situations of high intensity, such as during territorial conflicts or at dawn. According to this view, variation in use of the two modes can be seen as the result of variation in the intensity of the interaction, regardless of whether song is directed towards male or female listeners. This view might also predict a stronger response to serial songs, but provides no clear basis for predicting a change in response to the two modes over the course of the breeding season.

One obvious prediction of the hypothesis that serial songs are male directed is that males will preferentially use these song types in their interactions with other males. We should be able to use playback to test this prediction, because it simulates this type of interaction. The type of song used in response to playback was not recorded in our experiment, but these data were recorded by Weary et al. (1992). Nine of their subjects sang during both the 2-min period before playback began and during the first playback period. Of these, five sang serial songs during both periods, three sang repeat before playback began but switched to serial during the playback, and only one sang serial before and switched to repeat during playback (Fisher exact test, $P = 0.048$). Thus, redstarts show some tendency to respond to playback with serial songs, again indicating that this mode is more important in male-male interactions.

Acknowledgments.—We thank Johanne Mongrain and Darlene Miller for their field assistance, and Liz Date, Ross Lein, Jim Mountjoy, George Lozano, and Ken Yasukawa for their comments. Financial support was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to R.E.L. and by an NSERC postdoctoral fellowship to D.M.W.

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Received 12 May 1993, accepted 24 November 1993.

The Auk 111(3):734–739, 1994

Response of Male Brown-headed Cowbirds to Broadcast of Complete or Partial Flight Whistles

Alfred M. Dufty, Jr., and James K. Pugh[1]
Biology Department, Boise State University, Boise, Idaho 83725, USA

The vocal repertoire of male Brown-headed Cowbirds (*Molothrus ater*) during the breeding season is rich and varied, and includes several different vocalizations. The best-known cowbird vocalization, the species-typical song, consists of several low-frequency introductory notes followed by a high-frequency whistle (Friedmann 1929). A second vocalization heard throughout the breeding season is the flight whistle (FW). Cowbird FWs consist of two or more syllables that are largely pure tones, although some FWs may contain extensive frequency sweeps (Rothstein and Fleischer 1987, Rothstein et al. 1988). For example, the FW given by male cowbirds in our study population consists of two parts (Fig. 1). The first half is a single syllable of relatively pure tone, although it has rapid frequency sweeps at its beginning and end. The second half of the FW contains two syllables that always accompany each other in the order shown in Figure 1. The first of these syllables is brief and has an overall rise in frequency, while the second begins with a gradual frequency descent that ends as a pure tone over the last half of the syllable.

Most males have a single stereotyped FW, and most males in a given area share the same FW, producing FW dialects (Rothstein and Fleischer 1987). FWs are used in a variety of contexts: they are given in response to female vocalizations; they act as alarm calls; and they are produced during copulatory attempts (Rothstein et al. 1988, Dufty and McChrystal 1992). However, the most frequent behavior associated with flight whistles is, as the name suggests, flight. Cowbirds will give FWs when they are about to take flight, during the flight itself, and when landing (Friedmann 1929, Rothstein et al. 1988). Furthermore, all or only part of a FW may be produced (Rothstein and Fleischer 1987, Dufty pers. obs.). For example, male cowbirds near Boise, Idaho may perform only the first half, only the second half, or the full FW. Full FWs usually are presented in the sequence shown in Figure 1, but it is not uncommon for the two-syllable second half to be emitted first, followed by the first half (hereafter termed full FW [reversed]).

While working with cowbirds in upstate New York and Boise, one of us (A.M.D.) noted that, when a male cowbird flying into an area produced part of a FW, it often was answered with the remaining part by a male already in that area. The newcomer typically would alter his flight path to approach the resident, and additional social interactions frequently followed such vocal interplay.

Male cowbirds have breeding home ranges of up to 30 ha or more in size (Darley 1982, Dufty 1982a, Rothstein et al. 1984). Ranges are not defended in a way that provides exclusive use of an area for any given male (Dufty 1982b, Rothstein et al. 1986, Yokel 1989). Thus, several males may occupy overlapping

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[1] Present address: 4400 NW Walnut Blvd., Apt. 129, Corvallis, Oregon 97330, USA.