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## **Habituation, Recovery and the Similarity of Song Types within Repertoires in Red-winged Blackbirds (*Agelaius phoeniceus*) (Aves, Emberizidae)**

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### **Abstract**

Male red-winged blackbirds (*Agelaius phoeniceus*) respond to playback of conspecific song on their territories with the song spread, a graded aggressive display in which males extend their wings to expose their red epaulets while singing. We show that the intensity of song spread display declines with repeated presentation of one song type, and recovers when song types are switched. Recovery is greater for switches between song types that are acoustically dissimilar than for switches between song types that are acoustically similar. Recovery is no different for switches between two song types taken from the repertoires of different males than for switches between song types recorded from the same male. Analysis of acoustic features also indicates that song types recorded from different males are not more dissimilar than are song types from the same male. Our results do not support the idea that repertoires of red-winged blackbirds are composed of similar song types in order to facilitate individual recognition. Rather, repertoires may be constructed of dissimilar song types, so as to help maintain the response of listeners despite habituation.

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### **Introduction**

This study examines whether song types from repertoires of single individuals are more similar than are song types from repertoires of different individuals in red-winged blackbirds (*Agelaius phoeniceus*). The similarity of song types within repertoires bears on two topics of current interest: individual recognition by song, and the antihabituation effects of repertoires. We also investigate whether acoustic similarity between successive song types affects listener response.

Several authors have suggested that song repertoires ought to hinder individual recognition in birds (KROODSMA 1976; KREBS & KROODSMA 1980; FALLS 1982). One rationale is that if recognizing an individual requires learning each of his song types, then the memorization task becomes more difficult as the repertoire becomes larger. A second, parallel argument is that the more songs there are in a male's repertoire, the more likely some of them are to resemble songs of other males, making discrimination more difficult. Early comparisons of neighbour-stranger discrimination seemed to support the idea that repertoires hinder individual recognition, in that discrimination appeared weaker in species with large repertoires than in species with small repertoires (two to five song types) or only a single song type per male (SEARCY et al. 1981; FALLS 1982). More recently, however, strong neighbour-stranger discrimination has been shown in species with moderately large repertoires (e.g. STODDARD et al. 1990), and a comparative analysis of the species so far studied concluded that discrimination does not actually weaken as repertoire size increases (WEARY et al. 1992). Therefore, the arguments as to why repertoires should interfere with recognition must not apply to many species.

One way to escape the original arguments is to suggest that all the songs within an individual's repertoire share certain distinctive features, so that they are clumped in an 'acoustic space'. If so, then a listener could recognize an individual simply by learning the shared features of his song types, rather than by memorizing each song type separately, in which case the memorization problem would not worsen as repertoire size increases. Further, if all the songs within an individual's repertoire are clumped in terms of acoustic features, then differences between individuals could be maintained despite large repertoire sizes.

Recognition of an individual's song types by their shared features resembles how humans recognize voices and has been termed recognition by 'voice' characteristics (WEARY et al. 1990). Recognition by voice characteristics appears to operate in at least one bird, the great tit (*Parus major*). Here the songs within individual repertoires resemble each other in features such as duration and frequency (WEARY et al. 1990), and conditioning experiments have indicated that listeners can assign unfamiliar songs to the correct repertoires (WEARY & KREBS 1992). If being recognized is advantageous to singers, we might expect such distinctive voice features to be favoured; alternatively they might occur as nonadaptive consequences of individual peculiarities in experience during song learning or in song production and control mechanisms. A conditioning experiment performed with a second species, song sparrows (*Melospiza melodia*), found no evidence that subjects could assign unfamiliar song types to the correct repertoires (BEECHER et al. 1994), so it is unclear whether individual voice characteristics are common or uncommon across species.

Although assembling repertoires from similar songs may facilitate individual recognition, there may be competing advantages to assembling repertoires from dissimilar songs. Many hypotheses on the function of song repertoires in birds propose an advantage in terms of minimizing habituation in listeners (HARTSHORNE 1956; KREBS & KROODSMA 1980). These hypotheses suggest that the use of multiple song types may lessen a decay in some response that is beneficial to the singer, such as avoidance by rival males or courtship in females. There have

been a number of experimental demonstrations that repertoires affect habituation. For example, in great tits (KREBS 1976) and white-crowned sparrows (*Zonotrichia leucophrys*) (PETRINOVICH & PATTERSON 1982), there is less habituation in the aggressive response of territorial males to playback of multiple song types than to playback of single song types. In red-winged blackbirds (*Agelaius phoeniceus*), the aggressive response of males habituates for repeated playback of one song type, and recovers when song types are switched (YASUKAWA 1981 a). A similar pattern of habituation and recovery has been shown for courtship responses of captive females in swamp sparrows (*Melospiza georgiana*), red-winged blackbirds, and common grackles (*Quiscalus quiscula*) (SEARCY et al. 1982; SEARCY 1988 a, 1992). Exceptions have been found, for example, where no habituation occurs in response to single song types (SIMPSON 1984).

When habituation does occur, we might expect that response recovery would be greater between acoustically different song types than between similar ones. Studies with eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*) have shown that males are more responsive to switches between dissimilar than between similar songs (HORN & FALLS 1988; FALLS et al. 1990). If recovery is greater between dissimilar songs, and if the antihabituation effects of repertoires are advantageous, then we would expect selection to favour repertoires assembled from song types lacking shared features.

One of our two experiments tests whether response recovery is greater for switches between dissimilar song types than for switches between similar song types in red-winged blackbirds. YASUKAWA (1981 a) showed that the intensity of the song spread, a graded aggressive display, declines in male red-winged blackbirds in response to repeated playback of a single song type and recovers when song types are switched. We use the same playback method to determine whether recovery is greater when pre- and post-switch song types are acoustically dissimilar than when they are similar. This experiment bears on the question of whether assembling repertoires from dissimilar song types might have an advantage in maintaining response to song in listeners. It also bears on an assumption of the second experiment, that response recovery is proportional to song similarity as perceived by our subjects.

In our second experiment, we compare recovery for switches between two songs from a single repertoire to recovery for switches between two songs from repertoires of different individuals. Assuming that recovery is indeed proportional to song similarity, this experiment tests whether repertoires are assembled from similar songs. We also examine whether pairs of song types from within repertoires are more similar than pairs from different repertoires on an array of acoustical features. YASUKAWA (1981 a) previously found redwing song types are just as variable within repertoires as between individuals for five features; here we extend this type of analysis to a larger array of acoustical measurements.

## Methods

### Study Species

Red-winged blackbirds are territorial and polygynous. Male song functions both in defending the

territory against intrusion by other males (PEEK 1972; YASUKAWA 1981 a,b) and in stimulating courtship in females (SEARCY 1988 a). Multiple song types are superior to single song types in producing both effects (YASUKAWA 1981 a; SEARCY 1988 a). Songs usually consist of a series of unrepeatable introductory notes followed by a single syllable repeated in a trill; in addition there are sometimes one or more post-trill notes. Individual males have repertoires of two to eight song types, which are sung with eventual variety, i.e. a male repeats a single song type many times before switching to another (YASUKAWA 1981 a). There are a large number of song types within a population, each of which appears to be unique to a single individual. Specific song types do not appear to be used in specialized contexts or to perform specialized functions (SMITH & REID 1979).

### Playbacks

We performed two playback experiments, which we will call the same male/different male experiment and the similar song/dissimilar song experiment. Both experiments examined whether response of male red-winged blackbirds decreased over periods in which a given song type was played repeatedly, and whether response recovered when the song type was switched. The same male/different male experiment asked whether recovery was as great for a switch between two song types from the same individual as for a switch between two song types from different individuals. The similar song/dissimilar song experiment asked whether recovery was as great for two song types similar in acoustic structure as for two dissimilar song types.

The playback method was modified from one used by YASUKAWA (1981 a), in which he presented 8 min of one song type to territorial male red-winged blackbirds followed by 8 min of a second song type, both at 6 songs/min. YASUKAWA (1981 a) analysed a single behaviour in his subjects, the song spread, a posture in which male redwings expose their epaulets while singing (ORIAN & CHRISTMAN 1968). This is a graded display which signals aggressiveness (YASUKAWA 1978). YASUKAWA (1981 a) noted song spread intensity on a four-step scale and averaged scores for each 2-min playback period. Song spread intensity decreased across the four periods of playback of the first song type, though not significantly, and then increased significantly between the last playback period of the first song type and the first period of the second (YASUKAWA 1981 a).

We followed YASUKAWA (1981 a) in using 8 min of playback of one song type followed by 8 min of a second; however, YASUKAWA placed 1 min of silence between each 2 min of playback and we did not. We presented songs at 6 songs/min, so that in 8 min a song was repeated 48 times. This number of repetitions is greater than the mean of 20 found in natural bouts of redwing song (YASUKAWA 1981 a) but is well within the natural range (1–130 repetitions). We followed YASUKAWA (1981 a) and PEEK (1972) in dividing song spread intensities into four categories, but we simplified the category definitions by basing them solely on wing movements, as follows: (1) incipient – the wings remain folded against the body as the male sings, (2) low intensity – the wings are moved slightly away from the body, (3) moderate intensity – the wings are moved far enough away from the body so that a gap appears between the flight feathers and body, and (4) high intensity – the wings are fully extended from the body and bowed downwards, so that the bird assumes a disc-like form. Our methods differed from those of YASUKAWA (1981 a) in that intensity scores noted in the field were subsequently converted to measurements of wing extension so as to make the use of interval-level statistics legitimate. Wing extension was measured as the increase in the span of the trailing edge of the wing in song spread over the span in a normal perched posture, where the span of the trailing edge is the distance from the tip of the innermost secondary to the tip of the outermost primary. To find the correct conversions, wing measurements were made on five taxidermic mounts stuffed in varying intensities of song spread; the procedure was to score the mount on the intensity of its song spread according to the above criteria, and then measure the span of the rear edge of one wing. In addition, we measured wing span on one live bird, with wings at rest and with wings extended manually by us into positions mimicking song spreads of varying intensities. Using these procedures, we found that intensity scores of 1, 2, 3 and 4 corresponded to wing extensions averaging approximately 0, 2, 5 and 9 cm, respectively.

We played songs from a Marantz PMD221 cassette tape recorder and a Mineroff SME-SC-A9 speaker. The speaker was placed on a platform mounted on a pole approximately 1.5 m long which could be pushed into the substrate of a marsh. In each trial the platform was placed well within the boundaries of the subject's territory. The observer stood off the territory, usually at a distance of about 30 m from the speaker. Songs were played at an amplitude of 87 ( $\pm 2$ ) dB measured at 1 m. Experiments were performed at a number of sites in Crawford County, Pennsylvania.

Playback songs were recorded with a Marantz PMD221 cassette tape recorder, a Marantz EC-3S cardioid condenser microphone, and a Sony PBR-330 parabolic reflector. Birds were recorded on marshes located within 15 km of each other in Crawford County. The same male/different male experiment utilized 11 sets of playback songs, each set containing two song types recorded from one individual and one song type recorded from another individual on the same marsh. Within each set, there were two playback tapes: a same-male tape consisting of 8 min of song 1A (male 1 song type A) followed by 8 min of song 1B (male 1 type B), and a different-male tape consisting of 8 min of song 1A followed by 8 min of song 2A (male 2 type A). No male or song was used in producing more than one set, and thus 33 songs from 22 males were used altogether in this experiment. Tapes were never used in trials on the same marsh where the playback songs were recorded, so that subjects would not have any prior familiarity with the songs.

Eight sets of playback songs were used in the similar song/dissimilar song experiment. Each set contained one focal song, which was paired with a similar song type on one tape and with a dissimilar song type on a second tape. All songs within a set were recorded from different individuals. Songs were chosen by combing a library of about 60 songs for similar and dissimilar pairs. Similarity/dissimilarity was judged first by two acoustic measurements that seemed particularly salient to human observers: song duration and trill repetition rate (syllables per s in the trill). A second judgement was then made subjectively, i.e. certain pairs matched for duration and trill repetition rate were discarded because they sounded too different to humans. We did not find identical or even nearly identical song types produced by different individuals; rather our problem was to find pairs we considered even somewhat similar. Because of the difficulty of finding similar pairs, all similar pairs were used in two playback sets; for example, the pair Y1C/O1F was used in one set with Y1C as the focal song and O1F as the similar song, and in a second set with O1F as the focal song and Y1C as the similar song. All eight sets used different dissimilar songs.

The mean difference in duration between songs within similar pairs ( $0.10 \text{ s} \pm 0.05 \text{ SD}$ ,  $n = 4$ ) was significantly less than the mean difference within dissimilar pairs ( $0.44 \pm 0.20$ ,  $n = 8$ , Student's  $t = 3.29$ ,  $p < 0.01$ ). The mean difference in trill repetition rates was also significantly less within similar pairs ( $2 \text{ syllables/s} \pm 2$ ) than within dissimilar pairs ( $47 \pm 9$ ,  $t = 9.99$ ,  $p < 0.001$ ). This analysis shows that our similar songs were indeed more similar in these acoustic features than were our dissimilar songs.

Some of the songs were filtered using a Kronhite band-pass filter (model 3700) to remove low-frequency sound. If any one song was filtered for a set of songs, all songs in the set were filtered. Seven sets of same male/different male playbacks were performed in 1991 and four in 1992. Playbacks with all eight similar/dissimilar tape sets were performed in 1992.

The playback experiments were in some respects performed blind. For the same male/different male experiment, the observer (SC) was never told which tape represented which condition within each playback set, and we do not believe that humans can make the judgement by ear. For the similar/dissimilar tapes, humans can make the discrimination by ear, so here the observer was not told what the experiment was about (i.e. comparing recovery for similar and dissimilar pairs), nor what the prediction was (i.e. that recovery would be greater for dissimilar pairs).

Each playback tape was used in four trials with different males. For the same male/different male playbacks, 88 trials were performed ( $11 \text{ sets} \times 2 \text{ tapes/set} \times 4 \text{ trials/tape}$ ). A total of 78 subjects were used in this experiment; 10 males (that could be individually identified) were tested twice, once with a same-male tape and once with a different-male tape from another set. Note that all 44 trials done with one treatment (same male or different male) were done with different subjects, so that all are independent in this sense. For the similar/dissimilar experiment, a total of 64 trials were performed ( $8 \text{ sets} \times 2 \text{ tapes/set} \times 4 \text{ trials/tape}$ ), using 64 males. For both experiments, the trials with one set of playback tapes were performed on consecutive days, with the two tapes used alternately in random order. All trials were run between 0600 and 1000 h.

Our statistical analysis concentrates on mean responses to tapes, averaged over the four trials done with each tape. This procedure avoids the non-independence problem termed pseudoreplication by KROODSMA (1989). For the key test of whether recovery is greater for switches between different males than between same males, 11 mean recoveries for the different-male tapes are compared with 11 mean recoveries for the same-male tapes. For the test of whether recovery is greater for dissimilar than similar songs, we averaged the mean recoveries for each pair of tapes using the same pair of similar songs, e.g. we averaged responses to the O1F-Y1C and Y1C-O1F tapes. Therefore our sample size

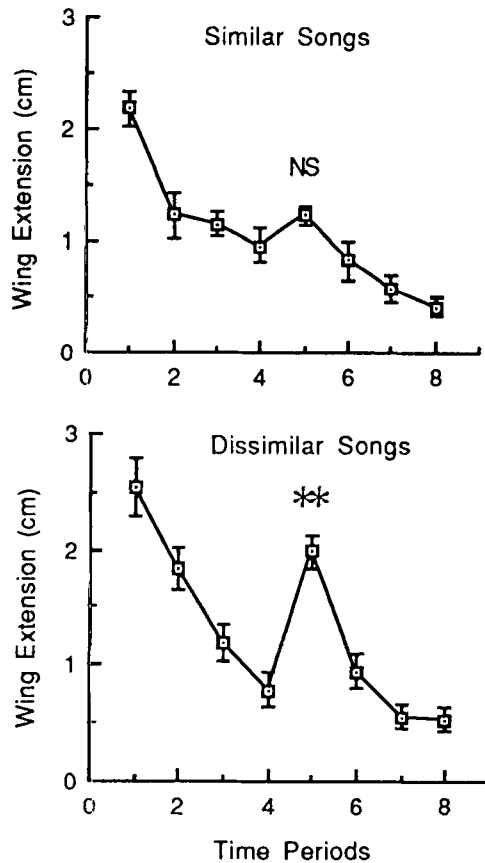


Fig. 1: Habituation and recovery of the song spread display in response to playback of either two similar song types or two dissimilar song types. Values are mean ( $\pm$ SE) wing extension for all song spread displays observed during 2-min periods. One song type was played during periods 1–4, followed in periods 5–8 by a second song type that was either acoustically similar to the first or acoustically dissimilar. The recovery of response between the fourth and fifth playback periods was not significant for the similar song playbacks ( $p > 0.05$  by a Wilcoxon matched pairs test) but was significant for the dissimilar song playbacks ( $p < 0.01$ )

for this comparison is four mean recoveries for similar songs versus eight mean recoveries for dissimilar songs. We use a one-tailed test for this comparison, because the direction of the expected difference is predicted (greater recovery for dissimilar songs than for similar). We tested for habituation by comparing responses during the first and last 2-min playback period with a given song type using Wilcoxon matched pairs tests. Here the response per playback tape (averaged across four subjects) is considered an observation; the 'n's given are numbers of pairs of untied observations. One-tailed tests are used because habituation is predicted to occur.

### Playback Results

#### Similar/Dissimilar Songs

Fig. 1 shows the response to the similar song playbacks. Mean wing extension

decreased across the first four playback periods, during which the first test song was played. The decrease between the first and fourth periods was significant (by a Wilcoxon matched pairs test,  $T = 0$ ,  $n = 8$ ,  $z = 2.53$ ,  $p < 0.01$  one-tailed). Response recovered slightly between the fourth and fifth periods (when the song type was switched), but the increase was not significant ( $T = 8.5$ ,  $n = 8$ ,  $z = 1.33$ ,  $p > 0.10$  two-tailed). Response declined again during the playback of the second song type; the decrease between the fifth and eighth periods was significant ( $T = 0$ ,  $n = 8$ ,  $z = 2.52$ ,  $p < 0.01$ , one-tailed).

Figure 1 also shows the response to the dissimilar song playbacks. Response again decreased during the first four playback periods ( $T = 0$ ,  $n = 8$ ,  $z = 2.52$ ,  $p < 0.01$ ) and during periods 5 through 8 ( $T = 0$ ,  $n = 8$ ,  $z = 2.54$ ,  $p < 0.01$ ). In this case, the recovery in response between the fourth and fifth periods was significant ( $T = 0$ ,  $n = 8$ ,  $z = 2.53$ ,  $p < 0.02$  two-tailed). More importantly, the magnitude of the recovery for dissimilar songs ( $1.20 \pm 0.19$  SE,  $n = 8$ ) was significantly greater than the recovery for similar songs ( $0.28 \pm 0.15$ ,  $n = 4$ ; Mann-Whitney  $U = 2.5$ ,  $z = 2.31$ ,  $p < 0.02$ , one-tailed).

#### Same Male/Different Male

Response to the same-male and different-male tapes (Fig. 2) showed the same basic pattern of habituation to repeated presentation of a single song type and recovery when song types were switched as observed in the previous experiment. Decrease in response between the first and fourth playback periods was significant for the same-male playbacks ( $T = 1.5$ ,  $n = 11$ ,  $z = 2.81$ ,  $p < 0.01$  one-tailed) and for the different-male playbacks ( $T = 0$ ,  $n = 11$ ,  $z = 2.94$ ,  $p < 0.01$  one-tailed). Habituation during playback of the second song type was also significant for both same-male playbacks ( $T = 0$ ,  $n = 11$ ,  $z = 2.94$ ,  $p < 0.01$ ) and for different-male playbacks ( $T = 0$ ,  $n = 11$ ,  $z = 2.94$ ,  $p < 0.01$ ).

Recovery between periods 4 and 5 was significant for both the switches between song types from the same males ( $T = 0$ ,  $n = 10$ ,  $z = 2.81$ ,  $p < 0.01$  two-tailed) and the switches between song types from different males ( $T = 0$ ,  $n = 11$ ,  $z = 2.94$ ,  $p < 0.01$  two-tailed). The magnitude of the mean recoveries was similar for same-male switches ( $0.62 \pm 0.13$ ,  $n = 11$ ) and different-male switches ( $0.76 \pm 0.10$ ,  $n = 11$ ), and was statistically indistinguishable (Mann-Whitney  $U = 48.5$ ,  $z = 0.79$ ,  $p > 0.40$ , two-tailed).

#### Methods for Song Measurements

We used a two-stage procedure to test for acoustic similarities between song types within repertoires: we first tested for differences in a large number of acoustic parameters with a lax alpha criterion, using these tests to erect hypotheses about what parameters might be similar within repertoires; we then tested these hypotheses with a stricter alpha criterion using a second collection of songs. (The alpha criterion is lax in the first tests in that it is not adjusted for the large number of tests being run.) The first, exploratory tests were done on 22 song types recorded from five males (four in 1989 and one in 1992). All males held territories in a marsh near the Pymatuning Laboratory of Ecology Housing Area in Linesville, Crawford County, Pennsylvania (SEARCY 1988b). The second collection of 33 songs were those used for the same male / different male playbacks.

Songs were digitized using MacSpeech Lab II hardware and software on a MacIntosh II computer.

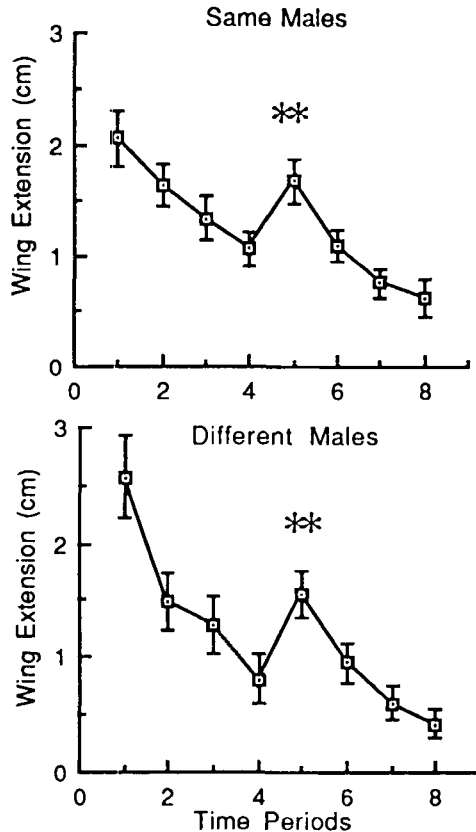


Fig. 2: Habituation and recovery of the song spread display in response to playback of either two song types from the same male or two song types from different males. Values are mean ( $\pm$ SE) wing extension for all song spread displays observed during 2-min periods. One song type was played during periods 1–4, followed in periods 5–8 by a second song type that was either from the same male or from a different male. The recovery of response between the fourth and fifth playback periods was significant for both the same-male playbacks and the different-male playbacks ( $p < 0.01$  in both cases by Wilcoxon matched pairs tests)

Most measurements were made using time and frequency markers manipulated on screen on spectrograms produced by the MacSpeech Lab software. Additional measurements were made on power spectrum plots (amplitude vs. frequency) produced using SoundScope software. Fifteen parameters were measured in each song in the first collection. These were (1) introduction length (s), (2) trill length (s), (3) total song length (s), (4) number of syllables in the trill, (5) number of notes in the introduction, (6) number of post-trill notes, (7) maximum frequency in the trill (Hz), (8) minimum frequency in the trill (Hz), (9) maximum frequency in the introduction (Hz), (10) minimum frequency in the introduction (Hz), (11) the ratio of introduction length to trill length, (12) trill repetition rate (number of syllables/s), (13) dominant frequency in the song (frequency with the greatest amplitude, in Hz), (14) dominant frequency in the introduction (Hz), and (15) dominant frequency in the trill (Hz). Time was measured to the nearest 0.01 s, maximum and minimum frequencies to the nearest 50 Hz, and dominant frequencies to the nearest 100 Hz.

One-way ANOVA was performed on each of the 15 parameters to determine whether there were consistent differences between individuals in the first collection of songs. Differences were accepted



Table 1:  $\bar{x}$  ( $\pm$ SD) of differences between pairs of song types from the same males and pairs from different males on three acoustic measures

	Minimum frequency trill (Hz)	Song duration (s)	Discriminant function
Same-male pairs	50 ( $\pm$ 90)	0.16 ( $\pm$ 0.11)	0.60 ( $\pm$ 0.60)
Different-male pairs	102 ( $\pm$ 123)	0.17 ( $\pm$ 0.09)	0.69 ( $\pm$ 0.40)
Student's <i>t</i>	1.14 (ns)	0.234 (ns)	0.429 (ns)

at the 0.05 level; however, because performing 15 tests obviously inflates our probability of finding differences at this level, these results are regarded as exploratory only. Those parameters showing differences in the exploratory tests were then measured in the second collection of songs. Each of the 11 sets of playback tapes contained two song types from one male and one song type from another male. We compared differences between the pairs of songs from the same male with the mean difference between the two pairs of songs from different repertoires within each set.

### Song Measurement Results

When one-way ANOVA was performed on the 15 song features in the first set of 22 song types, differences were found among the five males in two features, the minimum frequency in the trill ( $F = 4.23$ ,  $df$  4, 17) and song length ( $F = 3.01$ ,  $df$  4, 17). A canonical discriminant analysis was performed with these two variables to produce a single discriminant function; the raw canonical coefficients were 0.00446 for minimum frequency and 3.26 for song duration. The standardized canonical coefficient was higher for minimum frequency (1.07) than for song duration (0.570), showing that minimum frequency is the more important discriminating variable.

We then tested whether the three features, minimum frequency in the trill, song duration, and the discriminant function, could be used to discriminate pairs of song types from the same males from pairs from different males in the second collection of songs, the 33 song types used in the same male / different male playbacks. Differences between males were somewhat greater than differences within males on all three measures, but none of the differences approached statistical significance (Table 1).

### Discussion

Our experiments confirm that the response of male red-winged blackbirds to song habituates with repeated playback of any single song type, and that the response recovers when song types are switched. Further, we have shown that the magnitude of recovery depends on the degree of contrast between the pre- and post-switch song types: greater differences between the song types produce greater recovery. This demonstrates that recovery can be used to measure the degree of difference between two song types, as judged by red-winged blackbirds themselves. Using this measure, we have shown that male redwings treat two song types from the same male's repertoire as being just as different as two song types

from different males. Furthermore, analysis of acoustic features supports the conclusion that song types from the same repertoire are as different as are song types from different repertoires.

Our results provide no support for the idea that all the song types within a repertoire can be recognized by memorizing features common to all. If such common features existed in red-winged blackbirds, we would expect to see less recovery for switches within repertoires than for switches between repertoires, which was not the case. The test is not, however, conclusive; it may be that songs within repertoires differ on whatever characteristics determine recovery, but still resemble one another in a separate set of features that are used for individual recognition. We also found no evidence for common features in our acoustic analysis, but again the test is not conclusive, as we have not exhausted the list of features that might be used in individual recognition (and never could do so). A more conclusive test could be made with operant conditioning methods. We should point out that even if common features of songs within repertoires do not exist in some species, and recognition by voice quality is therefore impossible, birds in these species may still be able to recognize individuals with repertoires if their memories for song types are good enough. Recent experiments with song sparrows (*Melospiza melodia*) have indicated that males in this repertoire species do have formidable capacities for memorizing song types (STODDARD et al. 1992).

Our results better support the conclusion that male redwings assemble their repertoires from acoustically dissimilar song types. One functional explanation for this pattern is that the use of dissimilar song types helps to maintain the response of listeners in the face of habituation. Our results showed that recovery for switches between song types within repertoires was as high as, or at least not statistically distinguishable from, recovery for switches between song types from different repertoires. It would be more convincing if we had found that recovery was greater for switches within than between repertoires, in other words if we could show that song types from the same repertoires were more different than song types randomly chosen from different repertoires. There are constraints, however, on how different song types within repertoires can be, because all song types must have acoustic features within a range that will be recognized as conspecific by other red-winged blackbirds. For example, songs in our population have trill repetition rates that vary between 9 and 150 syllables per second (SEARCY 1990; unpublished data), and songs outside this range may not be recognized (BRENOWITZ 1983; SEARCY 1990). Therefore a male with, for example, six song types must construct all six with trill repetition rates within this range, which obviously constrains the mean difference between each pair of songs.

If switching between song types serves to maintain the interest of listeners, why do male red-winged blackbirds repeat one song type so many times (20 on average) before switching? Male red-winged blackbirds switch song types much more frequently than usual in one particular context: courtship of a receptive female (SEARCY & YASUKAWA 1990). In this situation, males repeat a given song type only three or four times on average between switches, and sometimes switch on every song. Female redwings can choose to mate with the owner of their own

territory or with another male (GIBBS et al. 1990, WESTNEAT 1992), so influencing choice in courtship must be of great importance to male fitness. Males, then, switch rapidly in a context in which maintaining listener response is of special importance, but this still does not explain why switching rates are so low in other circumstances. We can only suggest that rapid switching may have some cost, of which we are unaware.

A pattern of habituation to repeated presentation of the same song type and recovery when the song type is switched occurs even in species in which males possess only a single song type (SEARCY 1992). Thus habituation/recovery may be fundamental to song response systems, occurring independently of whether a species has a repertoire. Song repertoires may have evolved to take advantage of this built-in response pattern, or (if repertoires are the ancestral state) they may be maintained because of their advantage in exploiting the response pattern. Our present results constitute another demonstration of habituation/recovery, and further show that the magnitude of recovery depends on the difference between successive song types. This again makes the point that response to song is maintained by song diversity, in terms of both the number of song types and the differences between them.

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