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Avoidance of song matching in the Wood Thrush: a field experiment.—Song matching is a common form of vocal interaction in oscine species. It occurs when one bird, typically a territorial male, answers the song of another bird with a similar song. Matching has been reported for many species in which males sing with “eventual variety,” uttering one version of the territorial song a number of times before switching to another version: AAAA . . . BBBB . . . (e.g., Hinde 1958; Gompertz 1961; Lemon 1968a, b; Kroodsma 1971; Krebs et al. 1978). In contrast, matching has been reported for only a few species that sing with “immediate variety:” ABCDE . . . (e.g., Todt 1970, Verner 1975, Kroodsma 1979). It is not possible to say from present evidence whether matching is truly less common in birds that sing with immediate variety, but there is a clear need for studies of these species.

Wood Thrushes (*Hylocichla mustelina*) sing with immediate variety. My objective in the study reported here was to determine whether the results of an earlier study (Whitney and Miller 1983, see also Whitney 1985) of song matching in captive Wood Thrushes could be generalized to free-ranging birds. In the earlier work I presented each male with recordings of songs that were structurally similar to one of his own songs but that varied systematically from it in frequency (Hz). The results indicated that matching is related inversely to song similarity: the more similar the stimulus song was to the bird’s own song, the less it was matched, to the extent that subjects avoided matching their own songs and songs very similar to them.

Materials and methods.—A typical Wood Thrush song has three phrases, referred to as the A, B, and C phrases. The introductory A phrase consists of one or more low-pitched sounds, the middle B phrase is of loud flute-like notes, and the ending C phrase is usually a trill. B phrases are learned from conspecifics (Whitney and Miller 1987b) and can be classified into discrete types (Whitney and Miller 1987a, Whitney 1989). Use of the term “song type” in this paper refers to these B phrases. Each male has a repertoire of 2–8 B phrases, several of which may be different versions of the same type.

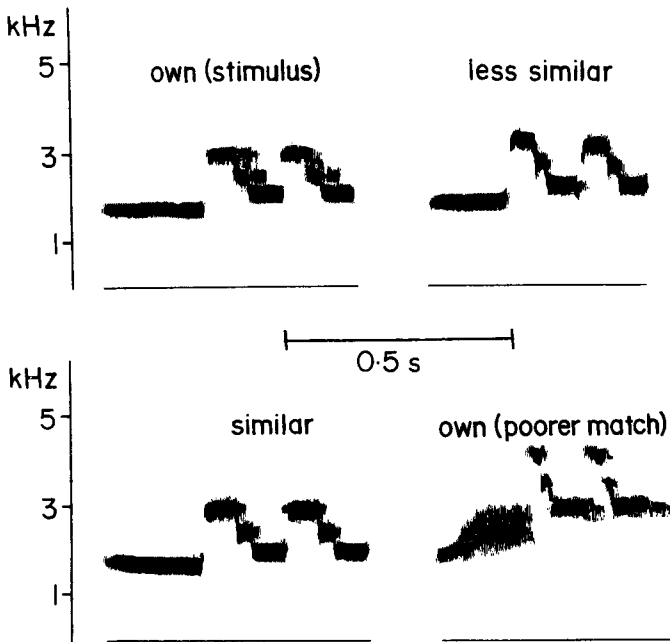


FIG. 1. Songs (each consisting only of a B phrase) presented to subject E, and a second song ("poorer match") of the same type in the subject's repertoire.

The experiment, done from 27 May to 21 June 1982 at 0530 to 0800 EDT, tested the response of territorial males to three songs: (1) a song from the subject's own repertoire, (2) a song of the same type as the subject's own song and very similar to it, and (3) another song of the same type but less similar to the subject's own song. Each stimulus song consisted only of a B phrase. I judged similarity of songs on the basis of frequency (Hz), requiring that each note of the "similar" song (category 2) be at least 200 Hz more similar in frequency than that of the "less similar" song to the corresponding note of the subject's own song. Fig. 1 shows the songs played to one subject.

The stimulus presented to each subject in the "own" song treatment was, of course, unique. For the "similar" and "less similar" treatments, however, subjects C and E (see Table 1) were presented with the same pair of songs, as were subjects D and F. Thus, the experimental design fell slightly short of Kroodsma's (1989) recommendations.

The general procedure was to broadcast a stimulus song from a loudspeaker in a subject's territory. Specific procedures were very similar to those used by Whitney and Miller (1983) in the earlier experiments with captive Wood Thrushes. On a given day the subject would hear 75 playbacks of one of the three stimulus songs. Each playback was of a single rendition of the song and occurred with a latency of 0.5–2.0 sec after the subject had completed one of his own songs. The subject was allowed to sing a randomly determined number (3, 4, 5, or 6) of songs between successive playbacks. For each subject the order of the experimental treatments was randomized, and the playbacks were done, one treatment per day, over a three to five day period. Thus, individual subjects were "blocks" in a randomized block

TABLE 1

RESULTS OF PLAYBACK EXPERIMENT (O/E = OBSERVED/EXPECTED NUMBER OF MATCHES; N = 75 PLAYBACKS FOR EACH TRIAL; CHI-SQUARE VALUES ARE FOR ONE DEGREE OF FREEDOM)

Subject	Own song			Similar song			Less similar song		
	O/E	χ^2	P	O/E	χ^2	P	O/E	χ^2	P
A	0.28	15.74	<0.001	0.20	23.73	<0.001	0.32	11.80	<0.001
B	0.77	1.40	N.S.	1.08	0.16	N.S.	1.33	2.63	N.S.
C	1.04	0.05	N.S.	0.97	0.03	N.S.	0.67	3.86	<0.05
D	0.65	2.42	N.S.	0.89	0.24	N.S.	0.91	0.16	N.S.
E	0.24	8.66	<0.005	0.86	0.36	N.S.	0.62	2.18	N.S.
F	0.16	10.12	<0.005	0.97	0.01	N.S.	0.38	6.30	<0.025
G	0.64	1.91	N.S.	0.85	0.33	N.S.	0.62	2.22	N.S.

design (e.g., Zar 1984). Anticipating a great deal of variability among subjects in their matching response (variability due perhaps in part to differences in breeding status, a variable that I did not measure), I chose this experimental design in order to increase statistical power in testing for a difference among song treatments.

I recorded the following data during each experimental trial: (1) the total number of songs sung by the subject, (2) the total number of renditions of the song of the same type as the stimulus song, and (3) the number of times the stimulus song was matched.

The subjects were seven males holding territories on or near the grounds of the Rockefeller University Field Research Center, Millbrook, New York. Immediately before doing the first playback to each male, I observed his behavior for at least 30 minutes and noted the locations of all song posts. I placed the loudspeaker on or near the ground within the area defended by song, using the same location for all trials. I controlled the loudspeaker from a distance of 15–20 m.

Throughout each experimental trial, I recorded the distance of the subject from the loudspeaker. To aid in estimation of distance I placed a pole 5 m from the loudspeaker.

The songs used for playback had been recorded with either a Uher Report IC tape recorder or a Sony TC-D5M cassette recorder, each equipped with a Dan Gibson P650 parabolic reflector and microphone. The playback system included a Sony Walkman Professional tape recorder, a Realistic 40W amplifier, and a Realistic 12-1853 loudspeaker.

The sonograms (Fig. 1) were prepared with a Macintosh Plus computer, a MacADIOS 411 hardware unit, a TTE 411AFS amplifier and anti-aliasing system, and MacSpeech Lab software (GW Instruments). The recording sample rate of the system was set at 10.416 kHz (according to which rate the maximum frequency displayed on a sonogram is 5 kHz), and the wide band filter (300 Hz) was used.

Results.—In most trials the subjects sang continually, except during flights. By allowing the subjects to sing a randomly determined number of songs before each playback, I established the expectation that by chance alone the number of playbacks answered with a given song type should be proportional to the overall frequency of occurrence of that song type.

In 18 of 21 trials the observed number of matches to the stimulus song was less than the expected number ($P < 0.002$, two-tailed binomial test). Several subjects were presented with the same songs in the “similar” and “less similar” treatments. The results were combined appropriately, resulting in 17 independent trials; the observed number of matches was less

than expected in 14 of these ($P < 0.02$, two-tailed binomial test). None of the stimulus songs was matched significantly more often than expected by chance, but seven were matched significantly less often (Table 1). Three of these seven songs were the subjects' own songs, one was a "similar" song, and three were "less similar" songs.

A Friedman's nonparametric analysis of variance for the randomized block design (Zar 1984) revealed no difference in the response to the three classes of songs ($\chi^2 = 2$, $df = 2$, $0.50 > P > 0.25$).

Having memorized the song repertoires of subjects D and F before starting the experiment, I was able to keep complete records of the songs they sang during each trial. As shown in Table 1, subject D did not match his own song significantly less than expected. Overall, however, his use of the four songs in his repertoire to answer his own song did deviate significantly from the expected ($\chi^2 = 12.48$, $df = 3$, $P < 0.01$). Similar analysis of the remaining three trials in which these two birds matched neither more nor less often than expected by chance revealed no further significant results.

According to the system used in classifying song types (Whitney and Miller 1987a), subject E had two songs in his repertoire of the same type as the stimulus songs. One of these songs was clearly a poorer match to the stimulus songs (Fig. 1). In all three trials the subject favored answering the stimulus with this song (Observed/expected number of matches = 1.66, 1.56, 1.49, respectively); with data combined for all trials, the result was significant ($\chi^2 = 12.52$, $df = 1$, $P < 0.001$).

Because each trial of the experiment involved 75 playbacks and lasted for 20 minutes or more, one can wonder whether the matching response of the subjects was consistent throughout this lengthy period. In an attempt to answer this question, I did two analyses. First, I calculated the ratio of the observed to expected number of matches for the first 20 playbacks and last 20 playbacks of each trial. If birds habituated during each trial by showing a decreasing tendency to match or avoid matching the stimulus song, this ratio should be closer to unity for the last 20 playbacks than for the first 20. In only 10 of the 21 trials, however, was the ratio closer to unity for the last 20 playbacks.

Second, I applied a runs test (Siegel 1956) to the series of matches and non-matches in each trial. In only three of 21 trials did the results deviate significantly from random: twice matches were clumped (similar and less similar songs for subject A; $P < 0.01$ and $P < 0.05$, respectively), and once they were spaced (similar song for subject B; $P < 0.001$).

Subjects were often out of my view during trials, but I was able to judge their closest approach to the loudspeaker as being in one of the following four categories: 0–5 m, 5–10 m, 10–20 m, and >20 m. In 14 of the 21 trials the subject approached to within 5 m of the loudspeaker. This response occurred in five of the seven trials in which the subject significantly avoided matching the stimulus song and in nine of the 14 remaining trials. Thus, subjects that avoided matching were no more likely than other birds to approach the loudspeaker closely.

Discussion.—The predominant vocal response to playback of recorded songs was avoidance of matching. In earlier research with captive Wood Thrushes, avoidance of matching occurred only when the stimulus song was identical or very similar to one of the subject's own songs (Whitney and Miller 1983). Using a computer to manipulate the frequency (Hz) of songs, I found that a shift of only 156 Hz eliminated the avoidance response of a subject to his own song. A shift of 468 Hz resulted in significant matching. From these results I proposed an inverse relationship between matching and song similarity.

This inverse relationship did not occur in the present research. The subjects were not consistent even in response to their own songs, only three of seven showing significant avoidance of matching (Table 1). Even more surprising was their response to "less similar" songs. Note for note, these songs differed from the birds' own songs by 200–600 Hz, yet

not a single subject matched significantly, and three avoided matching. I found only a single piece of evidence that free-ranging Wood Thrushes might sometimes match less similar songs of the same type: subject E had two songs in his repertoire of the same type as the stimulus songs and favored answering with the one that was a poorer match.

These experimental results, taken together with field recordings I have made of natural vocal interactions (Whitney, unpubl. data), indicate that avoidance of matching is common in free-ranging Wood Thrushes. Does avoidance of matching by territorial Wood Thrushes have functional significance? Could avoidance of matching in this species be functionally equivalent to the matching that occurs in many other species?

According to one hypothesis, matching allows a male to gain the attention of a specific rival (J.-C. Bremond, cited in Armstrong 1973). It seems unlikely that avoidance of matching functions in this way, since avoidance can only be detected over an extended period of time. Imagine two males, one with song A and the other with a similar song A'. If 40% of the songs delivered by the second male during a bout of singing are A', then it is expected that 60% of the first bird's renditions of A will not be matched when the two birds are singing independently. The first bird would require a large sample of answers to A in order to distinguish between this chance expectation and active avoidance.

Avoidance of matching is rarely so extreme in Wood Thrushes that no matching whatsoever occurs (Table 1 and unpubl. data). Perhaps, one might suggest, avoidance is a background against which a male suddenly matches several times in succession to gain the attention of a rival. Contrary to this idea, however, the temporal order of matches and non-matches to stimulus songs in the experiment was indistinguishable from the random expectation in 18 of 21 trials.

According to a recent hypothesis, matching functions not just to address a specific rival but to convey information about distance. Upon being matched, a bird would use its own song as a standard for estimating the extent of acoustic degradation—hence distance—of the other bird's song (Richards 1981, Falls et al. 1982, Morton 1982, McGregor and Krebs 1984). This hypothesis obviously cannot account for avoidance of matching, but the possibility remains that Wood Thrushes use a similar method of estimating distance. At present I have no evidence that avoidance of matching in Wood Thrushes represents anything more than a shortcircuiting of the neural mechanism that causes Wood Thrushes to sing with immediate variety. Presented with a stimulus song that is identical or very similar to one of his own, a male often behaves as if he has sung the song himself: he advances to the song that follows it in normal sequences (Whitney 1985).

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Diurnal resting metabolic rates of accipiters.—One of the major sources of error in estimating avian daily energy expenditure with time budgets is the estimate of maintenance metabolism (Weathers et al. 1984, Goldstein 1988, Nagy 1989). Resting metabolic rate (RMR) of a species of interest is often calculated from an allometric equation derived from measurements on other species. For example, Aschoff and Pohl's (1970) allometric equations for non-passerine birds are typically used to estimate active phase and resting phase RMR's of falconiforms (Tarboton 1978, Wakeley 1978, Koplín et al. 1980), but they do not include data from falconiforms. Wasser (1986) demonstrated that the relationship of RMR to body mass during the resting phase of falconiforms does not conform well to the predictions of Aschoff and Pohl (1970).

The RMR during the active phase of the daily cycle is approximately 24% higher than during the resting phase in some non-passerine species (Aschoff and Pohl 1970). Our ob-