Paul R. Martin · James R. Fotheringham · Laurene Ratcliffe · Raleigh J. Robertson

Response of American redstarts (suborder Passeri) and least flycatchers (suborder Tyranni) to heterospecific playback: the role of song in aggressive interactions and interference competition

Abstract Least flycatchers (*Empidonax minimus*) and American redstarts (*Setophaga ruticilla*) overlap in the use of food resources on their breeding grounds, promoting high levels of interspecific aggression by the socially dominant flycatcher. We examined the role of song in this interspecific aggression by using repeated-measures-designed playback experiments and observational data on induced aggressive interactions. Flycatchers were more likely to approach the speaker during presentation of redstart song than during intervals of no song or presentation of control song. Approach was close enough to enable visual contact with a singing redstart. In contrast, redstarts made significantly fewer flights following presentation of flycatcher song, when risk of flycatcher attack may be greatest. Reducing the number of flights likely reduces the risk of flycatcher attack on the redstart, as flycatchers do not attack stationary redstart models and are apparently dependent on cues from redstart flight for visual heterospecific recognition. Flycatcher-specific responses of redstarts and marked differences in song morphology rule out misdirected intraspecific aggression as a proximate or ultimate cause of interspecific response to song. Results indicate that song is an important component in aggressive interactions between these two species, and reflect the dominant role of the flycatcher in such interactions. Our results also illustrate the capacity for interspecific interference competition to influence behavior and heterospecific song recognition in two distant avian taxa.

Introduction

Song in birds is thought to serve primarily as an intraspecific signal (Kroodsma and Byers 1991). Interspecific response to song does occur, for example, in cases of interspecific territoriality (Orians and Willson 1964; Murray 1971, 1981; Cody 1974) and in predator-prey interactions (e.g., McPherson and Brown 1981; Møller 1992). In cases where overlap in resource use results in interspecific interactions, we should expect to see interspecific response to song, if such behavior confers net benefits to the responder. Such behavior has been documented in cases of adaptive interspecific territoriality (e.g., Catchpole and Leisler 1986), although it has been debated whether cases of interspecific territoriality reflect adaptive strategies of ecologically overlapping species (e.g., Cody 1969, 1974) or simply misdirected intraspecific aggression (e.g., Murray 1971, 1976, 1981).

Interspecific response to song associated with resource overlap often resembles response to conspecific song, and characteristically occurs between closely related species (e.g., congeners) with morphologically similar songs (e.g., Lanyon 1957; Cody 1974; Catchpole 1972, 1977, 1978; Rice 1978). Interspecific response to song between distantly-related competitor species (e.g., inter-familial) is rare, and has been documented in only a few species that exhibit interspecific aggression (Gorton 1977; Reed 1982).

The least flycatcher (*Empidonax minimus*) and American redstart (*Setophaga ruticilla*) provide an example of distantly related avian taxa that interact competitively through proximate interference (Sherry 1979; Sherry and Holmes 1988). These two species do

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not maintain mutually exclusive territories, however, least flycatchers demonstrate a high degree of aggression towards American redstarts (Sherry 1979; Sherry and Holmes 1988).

Similarities between these two species lie in their convergent morphologies related to food acquisition, foraging behaviors, and prey selection (Sherry 1979; Keast et al. 1995). Least flycatchers and American redstarts also share similar geographic breeding ranges (American Ornithologists' Union 1983), and within these breeding ranges overlap in macrohabitat use (to the point of frequent horizontal territory overlap; Sherry 1979; Bennett 1980; Sherry and Holmes 1988), and potentially in microhabitat use (Sherry 1979; Sherry and Holmes 1988). Thus, the high levels of aggression by the dominant flycatcher towards the redstart are hypothesized to originate from pressures of food resource overlap, with aggression helping to reduce this overlap through interference effects on behavioral and ecological strategies (Sherry 1979; Sherry and Holmes 1988).

Apart from ecological characteristics, least flycatchers and American redstarts are markedly different. Contrasts between the two species include taxonomic affiliation and phylogenetic history [least flycatchers are members of the suboscine passerine family Tyrannidae, while American restarts represent the oscine subfamily Emberizinae (Fringillidae)] (Sibley and Monroe 1990). The song structures of these two species also differ; least flycatchers sing a simple, stereotypic song across their range (Fig. 1A), with no reported variation within or among individuals (Briskie 1994), while American redstarts have complex songs and repertoires (Fig. 1B, C) consisting of two song modes (MacNally and Lemon 1985) and up to eight song types per individual (Lemon et al. 1985).

In this study we examined the role of song in interspecific aggressive interactions between least flycatchers and American redstarts. Using playback experiments, we tested two a priori hypotheses: (1) least flycatchers and American redstarts behave differently in response to each other's song versus no song stimulus and the song of a control species (black-capped chickadee, *Parus atricapillus*; Fig. 1D), and (2) response to each other's song differs from response to conspecific song. We also induced aggressive interactions between flycatchers and redstarts to gain more insight into the role song plays in interspecific interactions.

Methods

Study area

This study was conducted at the Queen's University Biological Station, Lake Opinicon, Ontario, Canada (44°30′ N; 76°23′ W). Densities of least flycatchers and American redstarts are relatively high (501–1000 pairs/100 km^2 for each species; P.R. Martin, unpublished work) in this area of 20 to 70 year old regrowth deciduous forest (P.R. Martin, unpublished work). The two species arrive at the study site from their wintering grounds in Central and South America and the Caribbean (American Ornithologists' Union 1983), and defend territories from early May onwards. Nest building begins in mid to late May, with young fledging by late June (P.R. Martin, unpublished work). Our study was carried out during periods of nest building through feeding of fledglings.

Experimental song playback

Playback setup

Song playback experiments were performed on 18 unmarked territorial male least flycatchers from 24 May to 3 June 1994, and 18 unmarked territorial male American redstarts from 11 June to 4

Fig. 1 Sonograms created from recordings of **A** least flycatcher, **B** American redstart singing in serial mode, **C** American redstart singing in repeat mode, and **D** black-capped chickadee. All recordings were made in the spring of 1993 at the Queen's University Biological Station, Lake Opinicon, Ontario, Canada
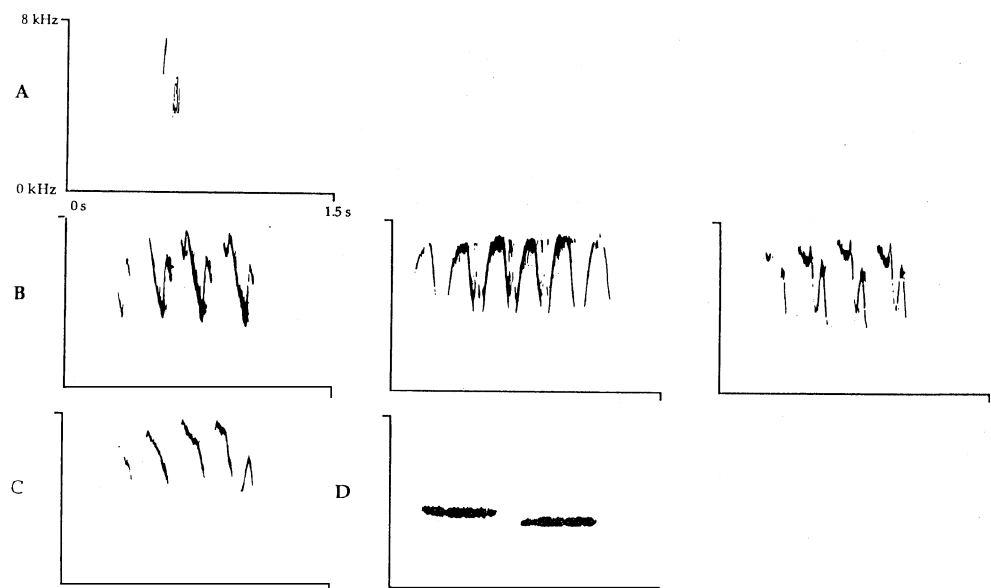
Table 1 Design of repeated measures song playback experiments presented to 18 territorial male least flycatchers and 18 territorial male American redstarts. Playback stimuli consisted of songs of least flycatchers, American redstarts, and black-capped chickadees (used as a control). Six playback tapes represented the six potential orders of stimuli

Stimulus	Duration	Behavioral observations used in analysis
No stimulus ("prestimulus")	1 min	yes
Stimulus 1	1 min	yes
No stimulus ("poststimulus 1")	1 min	yes
No stimulus (break)	2 min	no
Stimulus 2	1 min	yes
No stimulus ("poststimulus 2")	1 min	yes
No stimulus (break)	2 min	no
Stimulus 3	1 min	yes
No stimulus ("poststimulus 3")	1 min	yes

July 1994. Playback experiments were performed either in the morning (0530–1200 hours EST) or occasionally in the evening (1930–2000 hours EST), in all weather conditions judged not to affect the response of the birds or the ability of the observer to follow the birds (e.g., in high winds or heavy rains).

Each playback experiment lasted 11 min, during which focal males were followed continuously, and three song stimuli were broadcast (see Table 1). This repeated-measures design was used to control for inter-subject variation, environmental influences, factors of time and seasonality, and inter-observer bias. Song stimuli were presented to focal territorial males at fixed volumes from within their territories. A 3-min period with no song stimulus before the second and third stimuli controlled for carryover in response from the previous song stimuli (see Table 1). During pilot trials in 1993, we found that a 3-min break provided sufficient time for both least flycatchers and American redstarts to calm down after conspecific song stimulus (i.e., there was a decrease in behaviors characteristic of response to conspecific song, such as flights towards speaker and song rate). To further ensure that a 3-min break was ample time between playback stimuli, we tested for effects of song stimulus order, which would be expected if behavior in response to one stimulus carried over into the next (see the section on variables and analysis below). Occasionally, song stimulus would attract responding individuals other than the focal bird. In these cases, we could not distinguish whether the focal bird was responding to our song stimulus or to the presence of another responding individual. Consequently, the playback experiment was stopped and these data were not used in the analysis.

Male flycatchers and redstarts that defended territories in habitat favorable for continuous observations were chosen preferentially for playback experiments, although within this group we selected males at random. For each territorial male, we placed a speaker (Sony directional speaker, Model SRS-77G) and playback walkman (Sony Professional, Model WM-D3) within its territory, 1–3 m above the ground. One observer recorded all of the movements, vocalizations, and the estimated locations of the focal male relative to the speaker and the ground, using a lapel microphone (Sony Model ECM-144) and walkman (Sony Professional, Model WM D6-C). The observer for half of the experiments was J.R.F., while the observer for the other half was P.R.M. For most of the experiments, flagging tape was placed on two sides of the speaker at a distance of 5 m to assist in distance estimation. In all cases the observer estimated distance and heights to the nearest meter. Behavioral data (described below) were gathered and analyzed for seven 1-min intervals during the playback experiment (Table 1): during the first minute of the playback experiment preceding any song stimulus, during the

1-min presentation of each of the three song stimuli, and during the 1 min immediately following presentation of each of the three song stimuli.

Song stimuli

The three song stimuli consisted of songs of least flycatcher, American redstart, and black-capped chickadee (control), recorded from the Lake Opinicon area in 1993. Multiple replicates (two different songs from three individuals of each species) were used to obviate concerns regarding the external validity of playback experiments (see Kroodsma 1989). To make a playback tape, one of the six songs from each species was selected at random and repeated. Thus, all American redstart song stimuli consisted of repeat mode songs only. Songs were recorded from distances of <5 m using an Audiotechnica AT815a "shotgun" microphone and a Sony Professional WM-D3 cassette recorder. To create playback tapes, songs were filtered (0–2 kHz to 0 dB) and amplified (to a similar level for all songs) using SoundEdit, a sound analysis package for Macintosh computers. Song rates were selected from data in the literature describing average song rates for the three species. The song rates used were 49 songs/min for least flycatchers (Davis 1959; Briskie 1994), 12 songs/min for American redstart (Ficken and Ficken 1970), and 10 songs/min for black-capped chickadee (Shackleton et al. 1992). We used six playback tapes representing the six potential orders of song stimuli. The selection of playback tapes was block-randomized (see below for control of other potential effects of order).

Black-capped chickadee song was used as a control in the experiment to compare response of least flycatchers and American redstarts to song of another prominent forest passerine in the area. The black-capped chickadee inhabits a broad range of forested habitats in the study area (P.R. Martin, unpublished work) and frequently overlaps territories of both focal species. Least flycatchers have been observed attacking black-capped chickadees in the study area (P.R. Martin, personal observations), and thus black-capped chickadees provide a test of differential aggression towards this species versus the American redstart. Black-capped chickadees, however, may provide an unequal control for flycatchers versus redstarts, given that redstarts have not been observed to attack chickadees on our study sites. Such a case, however, was inevitable as least flycatchers have been observed attacking every similar-sized or smaller passerine with which it commonly overlaps territories (authors, personal observations; see also Sherry 1979; Briskie 1994), and thus a control passerine species that was not attacked by both redstarts and flycatchers was not present on our sites.

Variables and analysis

Recordings of observations of focal males during playback experiments were transcribed for 5-s intervals. From these transcriptions, mean values were calculated for 16 variables for least flycatchers, and for 15 variables for American redstarts, covering aspects of distance to speaker, height above ground, flights, vocalizations, and latencies (Table 2). Variables were selected on the basis that they illustrate response of least flycatchers and American redstarts to vocal stimuli (cf. Ficken 1962; Ficken and Ficken 1970; MacNally and Lemon 1985; Briskie 1994). Mean values for variables were calculated for seven 1-min intervals: prestimulus, stimulus-black-capped chickadee, post stimulus-black-capped chickadee, stimulus-American redstart, poststimulus-American redstart, stimulus-least flycatcher, poststimulus-least flycatcher (Table 1).

We used two-factor analysis of variance tests (ANOVAs) to test for effects of the order of song stimuli on observed behavioral responses (i.e., interactions between playback interval and order of stimuli). After examining for potential effects of order, we tested the two a priori hypotheses: (1) least flycatchers and American

Table 2 Behavioral variables used to measure subject response to playback during the seven 1-min intervals

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1. Minimum distance to speaker (m)
2. Mean distance to speaker (m)
3. Mean height above ground (m)
4. Number of flights
5. Number of flights towards speaker
6. Number of flights over speaker
7. Number of flights > 3 m in length
8. Number of flights ⩽ 3 m in length
9. Number of sallies (i.e., indirect flights that circle back; used in foraging)
10. Number of songs
11. Number of calls
12. Number of twitters (least flycatcher only; see Briskie 1994)
13. Number of cases of bill snapping
14. Latency to flight (nearest 5-s interval)
15. Latency to flight towards speaker (nearest 5-s interval)
16. Latency to vocalization (nearest 5-s interval)

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redstarts respond to each others' song, and (2) response to each other's song differs from response to conspecific song.

To test the first a priori hypothesis, we compared behaviors during control intervals (intervals of no song, and intervals during and after black-capped chickadee song) with behaviors during experimental intervals (intervals during and after the opposite species' song). Behavioral variables were numerous and often correlated with each other. Thus we collapsed 16 and 15 behavioral variables into six and five components for least flycatchers and American redstarts, respectively, using principal components analysis (PCA) (correlation matrix, equamax rotated axes). The large number of components was necessary to describe behaviors due to the broad distribution of explained variance across components (Tables 3 and 4). We then used the principal component scores in a series of block-randomized (on individuals), type III ANOVAs. Song stimulus and poststimulus intervals were compared separately to avoid ANOVAs comparing intervals that were not testing our hypothesis. Thus, for least flycatchers and American redstarts, six and five ANOVAs, respectively, tested for differences between intervals of no song (prestm − control), black-capped chickadee song (blcc − control), and opposite species song (experimental) with respect to each prin-

cipal component. The same number of ANOVAs (6 and 5 for flycatchers and redstarts, respectively) separately tested for differences between intervals of no song (prestm − control), the minute following black-capped chickadee song (postblcc − control), and the minute following the opposite species song (experimental) with respect to each principal component. In cases where ANOVAs were significant following a Bonferroni correction for multiple comparisons (12 and 10 comparisons for flycatchers and redstarts, respectively), Tukey's post hoc tests tested for differences specifically between the experimental intervals (amre/postamre or lefl/postlefl) and the two control intervals (prestm and blcc/postblcc) with respect to the principal component examined. In the interests of saving space, we limit our discussion to those variables where the post hoc tests rejected the null hypothesis.

To test the second a priori hypothesis, we compared response of focal species to conspecific song with response to song of the opposite species. Principal components could not be used for this comparison, as they were based on behaviors excluding conspecific playback intervals. Instead we compared responses to conspecific song versus the opposite species' song using behavioral variables that best characterized the principal component of interest (cf. Table 3; 4). These comparisons allowed us to assess whether response to the opposite species song differed from response to conspecific song for a given behavioral variable.

Inducement of aggressive interactions

To provide insight into how vocalizations may function in interspecific interactions, we broadcast American redstart song to attract male redstarts into close proximity of territorial male least flycatchers and recorded observations with respect to aggressive interactions. The reciprocal test of attracting least flycatchers into close proximity of redstarts was not undertaken because studies of these two species have documented only a one-way aggressive relationship, with the flycatcher always being dominant, even within territories defended by American redstarts (Sherry 1979; Sherry and Holmes 1988; authors, personal observations). We selected vocal territorial male least flycatchers between 0600 and 1200 hours, 9 June–23 June 1994. We then broadcast American redstart song, as in the playback experiments, from within the flycatcher's territory (usually underneath the bird). If no redstarts approached to within a 10-m horizontal radius of the speaker, we stopped broadcasting redstart song and a new focal least flycatcher was chosen. Upon

Table 3 Factor loadings, eigenvalues, and percentage of variance explained by principal components derived from a principal components analysis (PCA) on behavioral data from playback experiments involving 18 territorial male least flycatchers. Data used in PCA were gathered during control and experimental treatments (data gathered during conspecific treatments were not used in the PCA). Factor loadings for principal components > |0.70| are in boldface

Behavioral variable	Factor loadings for principal components where factor loadings > |0.20|					
	PC1	PC2	PC3	PC4	PC5	PC6
Min. distance to speaker	–	–	**0.95**	–	–	–
Mean distance to speaker	–	–	**0.97**	–	–	–
Mean ht. above ground	–	–	–	–	**−0.79**	–
Flights	**0.77**	0.27	–	–	0.44	–
Flights towards speaker	0.28	**0.85**	–	–	–	–
Flights over speaker	−0.21	**0.70**	–	–	–	–
Flights > 3 m in length	0.38	0.65	–	0.29	−0.24	0.25
Flights ⩽ 3 m in length	0.65	–	–	–	0.67	–
Sallies	0.32	–	0.24	–	0.56	–
Songs	–	–	–	**−0.86**	–	–
Calls	–	–	−0.38	0.38	–	0.36
Twitters	**0.81**	–	–	–	–	–
Bill snapping	–	–	–	–	–	**0.86**
Latency to flight	**−0.72**	−0.30	–	–	–	–
Latency to flight tow. speaker	−0.21	**−0.77**	–	–	–	–
Latency to vocalization	–	–	–	**0.82**	–	−0.21
Eigenvalue	4.1	2.3	1.7	1.6	1.2	1.1
% Variance explained	25.9	14.4	10.6	10.1	7.2	6.6

Table 4 Factor loadings, eigenvalues, and percentage of variance explained by principal components derived from a PCA on behavioral data from playback experiments involving 18 territorial male American redstarts. Data used in PCA were gathered during control and experimental treatments (data gathered during conspecific treatments were not used in the PCA). Factor loadings for principal components > |0.70| are in boldface

Behavioral variable	Factor loadings for principal components where factor loadings > |0.20|				
	PC1	PC2	PC3	PC4	PC5
Min. distance to speaker	–	–	**0.94**	–	–
Mean distance to speaker	–	–	**0.93**	–	–
Mean ht. above ground	–	–	0.62	−0.33	–
Flights	0.34	**0.92**	–	–	–
Flights towards speaker	**0.87**	–	–	–	–
Flights over speaker	0.49	–	−0.24	–	0.59
Flights >3 m in length	**0.82**	–	–	0.21	–
Flights ≤3 m in length	–	**0.95**	–	–	–
Sallies	–	0.69	–	–	–
Songs	–	–	–	**−0.90**	–
Calls	–	–	−0.22	–	**−0.77**
Bill snapping[a]					
Latency to flight	−0.46	−0.55	–	–	–
Latency to flight tow. speaker	**−0.85**	–	–	–	–
Latency to vocalization	–	–	–	0.89	–
Eigenvalue	3.5	2.3	2.1	1.8	1.1
% Variance explained	25.1	16.1	14.9	13.1	7.6

[a]No cases of bill snapping observed

response of a redstart to within 10 m of the speaker, we continued to broadcast redstart song for 15 min ($n = 1$) or until the redstart was displaced from a perch by the least flycatcher ($n = 10$). We placed flagging tape on two sides of the speaker at a distance of 10 m to assist in distance estimation.

We noted observations on the aggressive interactions that resulted after response of the redstarts to playback. These included latency to attack by least flycatcher (after response of the redstart to within 10 m of speaker), height and behavior of both redstarts and flycatchers prior to attack, distance of flight to attack, and outcome of attack (e.g., redstart retreated, flycatcher remained vocal in area).

Results

Experimental song playback

Order effects

We found no significant effects of order for all behavioral variables, with one exception (number of sallies by least flycatchers, $F = 2.36$, $df = 6{,}5$, $P = 0.001$), indicating that there was no effect of temporal position of each stimulus relative to the others for all behavioral variables except the one. For this variable, flycatchers reduced the frequency of sallies during intervals of control songs and the minute immediately following for all orders where control intervals followed redstart or flycatcher intervals (i.e., control was the second or third stimulus).

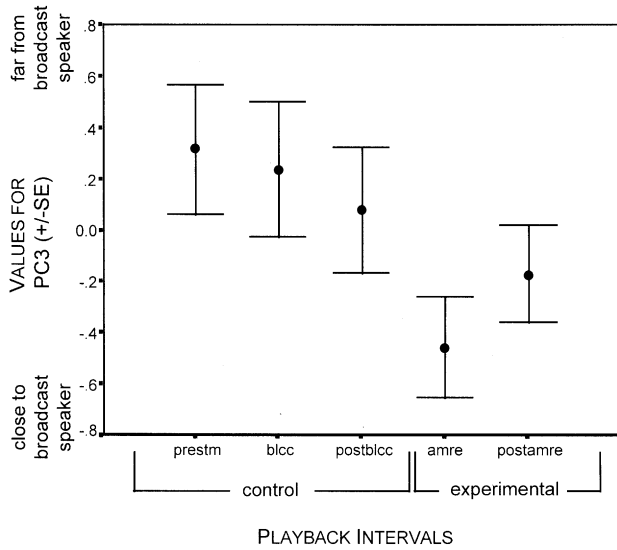#### Playback experiments on least flycatchers

Territorial male flycatchers responded to American redstart song by approaching the broadcast speaker (Table 5; Fig. 2). Principal component 3 describes dis-

Table 5 Results of analysis of variance tests (ANOVAs) performed on six principal components derived from principal components analysis (PCA) on behavioral data from playback experiments involving 18 territorial male least flycatchers. Data used in PCA were gathered during control and experimental intervals (not conspecific intervals). Table 3 describes the principal components in detail. ANOVAs were performed on "stimulus intervals" (i.e., *prestm* [the first minute of playback before any stimulus], *blcc* [1 min black-capped chickadee (control) song], *amre* [1 min American redstart song] separately from "poststimulus intervals" (i.e., *prestm*, *postblcc* [1 min immediately following black-capped chickadee (control) song], *postamre* [1 min immediately following American redstart song]

Principal component	*F*	*P*
Stimulus intervals (prestm; blcc; amre)		
PC1	0.04	0.96
PC2	0.97	0.39
PC3	8.74	0.001**
PC4	0.13	0.54
PC5	0.16	0.78
PC6	0.20	0.83
Poststimulus intervals (prestm; postblcc; postamre)		
PC1	0.16	0.86
PC2	0.34	0.71
PC3	3.45	0.043 n.s.
PC4	0.43	0.65
PC5	0.40	0.67
PC6	0.42	0.66

**$P < 0.05$, after Bonferroni correction for multiple comparisons; n.s. indicates no significance after Bonferroni correction for multiple comparisons

tance of least flycatchers from the broadcast speaker (Table 3), and showed significantly lower values during intervals of American redstart song compared with intervals of control song and no song (Fig. 2). This pattern was not significant for the minute following redstart song, indicating that least flycatchers did not

	prestm	blcc	postblcc
amre	.002**	.005**	----
postamre	.034**	-----	.38

Fig. 2 Mean values of principal component 3 (± SE) describing distance of territorial male least flycatchers to broadcast speaker (cf. Table 3) during control and experimental playback intervals (*n* = 18 flycatchers). The results of Tukey's post hoc tests (*P* values) are presented below the graph; ** values for PC3 differed significantly (*P* < 0.05) between experimental intervals (*amre, postamre*) versus control intervals (*prestm, blcc, postblcc*). Figure does not represent order of stimuli (see Table 1). Playback interval abbreviations are: the first minute of playback before any of the stimuli (*prestm*), 1 min black-capped chickadee (control) song (*blcc*), and the minute immediately following (*postblcc*), 1 min of American redstart song (*amre*), and the minute immediately following (*postamre*)

remain as close to the speaker once redstart song had stopped.

Response to songs of American redstart was similar to response to conspecific song with respect to distance of approach of the song source (Fig. 3). Minimum approach to the broadcast speaker was closer during intervals of conspecific song, with differences between conspecific and redstart song intervals approaching significance (*t* = 2.2, *df* = 17, *P* = 0.047, two-tailed, paired *t*-test; not significant with Bonferroni correction for multiple comparisons).

Playback experiments on American redstarts

Territorial male redstarts responded to least flycatcher song by decreasing their frequency of flights (Table 6; Fig. 4). Principal component 2 describes the number of flights (small flights, sallies, latency to flying) (Table 4), and showed significantly lower values (fewer flights) during the minute following least flycatcher song compared with the minute following control song
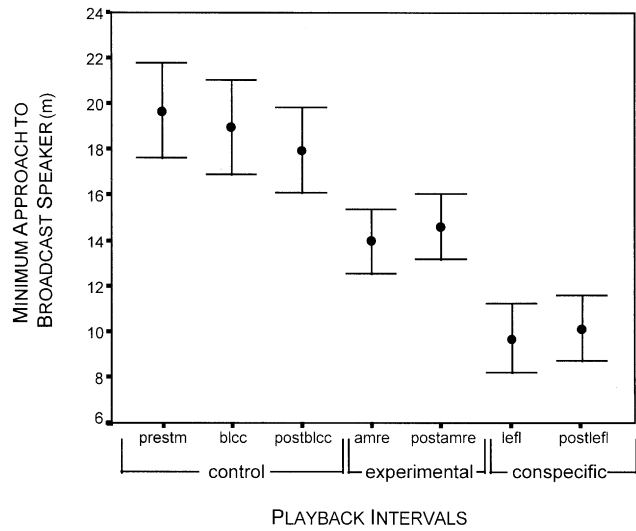

Fig. 3 Minimum approach (m) to broadcast speaker (mean ± SE) of territorial male least flycatchers during control, experimental, and conspecific playback intervals (*n* = 18 flycatchers). Figure does not represent order of stimuli (see Table 1). New playback interval abbreviations are: 1 min of least flycatcher song (*lefl*), and the minute immediately following (*postlefl*). See Fig. 2 caption for other playback interval abbreviations

Table 6 Results of analysis of variance tests (ANOVAs) performed on six principal components derived from PCA on behavioral data from playback experiments involving 18 territorial male American redstarts. Data used in PCA were gathered during control and experimental intervals (not conspecific stimulus intervals). Table 4 describes the principal components in detail. ANOVAs were performed on "stimulus intervals" (i.e., *prestm, blcc, lefl* [1 min least flycatcher song] separately from "poststimulus intervals" (i.e., *prestm, postblcc, postlefl* [1 min immediately following least flycatcher song]). See Table 5 caption for other playback interval abbreviations

Principal component	*F*	*P*
Stimulus intervals (prestm; blcc; lefl)		
PC1	0.23	0.80
PC2	1.45	0.25
PC3	1.11	0.34
PC4	1.12	0.34
PC5	2.53	0.095
Poststimulus intervals (prestm; postblcc; postlefl)		
PC1	0.25	0.77
PC2	4.67	0.004**
PC3	0.43	0.50
PC4	2.06	0.050 n.s.
PC5	2.91	0.016 n.s.

**P* < 0.05, after Bonferroni correction for multiple comparisons; n.s. indicates no significance after Bonferroni correction for multiple comparisons

and intervals of no song (Fig. 4). ANOVAs examining principal components 4 and 5 approached statistical significance (Table 6); however, post hoc tests did not suggest a response to the opposite species song.

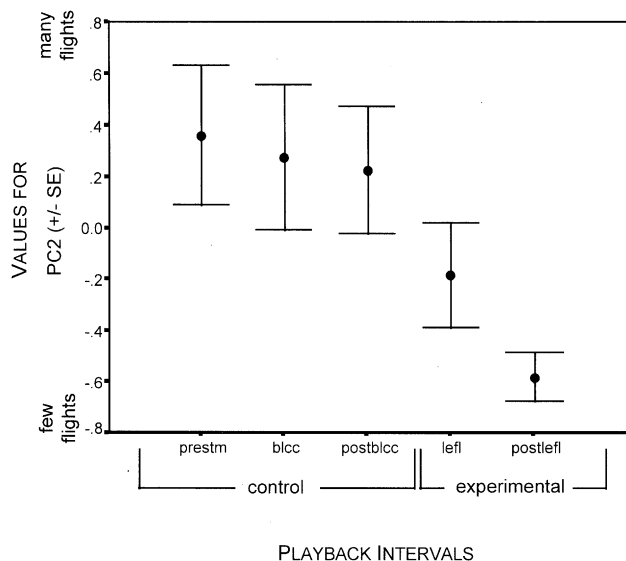Response of redstarts to least flycatcher song was opposite to response to conspecific song with respect to

	prestm	blcc	postblcc
lefl	.27	.39	----
postlefl	.005**	-----	.018**

Fig. 4 Mean values of principal component 2 (± SE) describing frequency of flights (cf. Table 4) of territorial male American redstarts during control and experimental playback intervals (n = 18 redstarts). The results of Tukey's post hoc tests (P values) are presented below the graph; ** values for PC2 differed significantly ($P < 0.05$) between experimental intervals (*lefl*; *postlefl*) versus control intervals (*prestm*; *blcc*; *postblcc*). Figure does not represent order of stimuli (see Table 1). See Fig. 2 and 3 captions for playback interval abbreviations

to number of flights during poststimulus intervals (Fig. 5). While American redstarts decreased the number of flights immediately following least flycatcher song, they increased the number of flights when presented with conspecific song. During the minute following conspecific song, redstarts exhibited frequencies of flights comparable to control intervals (Fig. 5).

Induced aggressive interactions

American redstarts were displaced from their perches or chased in the air by least flycatchers in 10 of the 11 trials that drew male redstarts to within 10 m of the broadcast speaker. In these ten induced attacks, the mean time to attack (after the redstart had approached to within 10 m of the speaker) was 2 min 26 s (range 0 to 8 min 10 s). Redstarts were attacked either immediately following a flight (n = 7 birds) or in mid-air as they flew towards the speaker (n = 3 birds). The height of the redstarts when attacked was variable, averaging 7.0 m above the ground (range 2.5–15 m). Redstarts were generally quiet when responding to redstart song, although in one case when two males responded to the stimulus, the vocal bird was attacked.
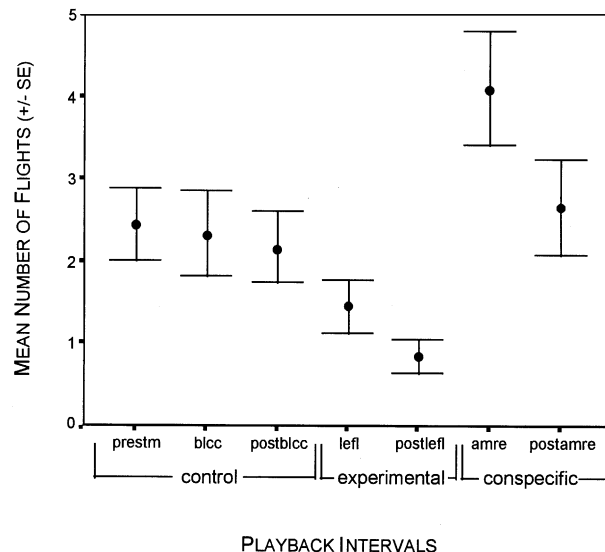

Fig. 5 Mean number of flights (± SE) made by territorial male American redstarts during control, experimental, and conspecific playback intervals (n = 18 redstarts). Figure does not represent order of stimuli (see Table 1). See Fig. 2 and 3 captions for playback interval abbreviations
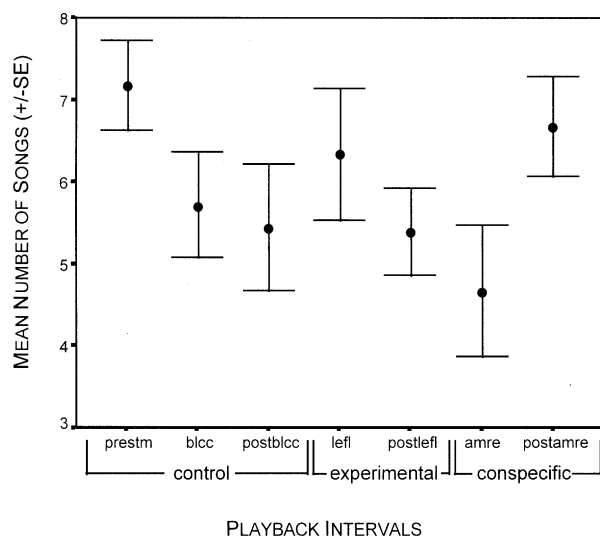

Fig. 6 Mean number of songs (± SE) sung by territorial male American redstarts during control, experimental, and conspecific playback intervals (n = 18 redstarts). Figure does not represent order of stimuli (see Table 1). See Fig. 2 and 3 captions for playback interval abbreviations

Typically, least flycatchers were relatively quiet immediately prior to attacking redstarts. Mean height prior to attack was 9.2 m (range 5–18 m), while the distance of flights to attack was often large, averaging 10.5 m (range 3–22 m). Attacks usually consisted of simply displacing the redstart from the perch, with the redstart retreating in every case. Occasionally redstarts were pursued in flight (n = 3 birds), but only if originally attacked in flight. These pursuits ranged from 5 m to at least 12 m. In one case, the redstart did not retreat

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from its perch, resulting in the flycatcher apparently hitting the redstart, fluttering its wings, and remaining in contact for almost a full second. The outcome of the attacks was always the eventual displacement of the redstart. Flycatchers usually remained in the immediate area (15 m radius) following attacks for several seconds, sometimes longer, often increasing their song rates.

Discussion

As previously reported (Sherry 1979; Sherry and Holmes 1988), least flycatchers were dominant in all interactions with American redstarts, and behaved as such during playback experiments. When presented with redstart song, least flycatchers responded aggressively, approaching the song source. This behavior would facilitate visual location and subsequent attack of a redstart within the flycatcher's territory.

The minimum approach distance of flycatchers to the broadcast speaker during redstart song was still relatively far (mean 14.0 m; range 5–27 m). Minimum speaker approach distance during redstart song, however, was not significantly different from the distance of flycatchers from redstarts when flights to attack were initiated (mean 10.5 m; range 3–22 m) ($P > 0.10$, Mann-Whitney U-test). This suggests that approach of least flycatchers to the broadcast speaker was close enough to enable visual contact with a singing redstart.

American redstarts responded to least flycatcher song by decreasing their frequency of flights (Figs. 4 and 5), which may function as a defensive behavior in flycatcher-redstart interactions. Observational data suggest that flycatchers are dependent on redstart flight for visual recognition in interspecific encounters. All redstarts observed being attacked by flycatchers were attacked immediately following ($n = 7$ birds) or during ($n = 3$ birds) a flight, (redstarts flew on average once every 14.6 s during conspecific song stimulus; cf. Fig. 5). In addition, when flycatchers were presented with a stationary model of an adult (>2 years old) male redstart coupled with song stimulus, none attacked the model, despite artificial movement of the model's tail and close proximity of the flycatchers ($n = 3$ territorial males). Redstarts, however, responded aggressively to the same model presentation ($n = 3$ territorial males). On one occasion, an adult male redstart, responding to the model, was attacked by the flycatcher (immediately following a flight), which ignored the adjacent redstart model. These observations suggest that flycatchers use cues associated with redstart flights for visual recognition, and do not recognize stationary redstarts.

In the playback experiments, the decrease in the frequency of redstart flights was most prominent immediately following least flycatcher song stimulus (Figs. 4 and 5). The flycatcher song would indicate the presence of a flycatcher within the redstart's territory; however, it also provides information on the location and movements of the flycatcher (simulated by broadcast speaker) for the entire minute of song stimulus. Knowing the location and movements of a potential attacker (i.e., the flycatcher) would likely reduce the risk of attack associated with its presence, and thus explain a weaker response of redstarts during flycatcher song stimulus. During the minute following flycatcher song, increased risk of flycatcher attack on redstarts associated with a lack of knowledge of the flycatcher's location and movements likely resulted in a decrease in redstart flights. Qualitative data from flycatcher-redstart interactions found flycatchers to have reduced song rates preceding attack flights on redstarts, also suggesting a reduction in risk of flycatcher attack associated with periods of flycatcher song stimulus.

With least flycatchers using redstart song as a cue in aggressive interactions, we might expect redstarts to decrease song rates when presented with flycatcher songs. Such a pattern was evident; redstarts reduced song rates in the minute following flycatcher songs as compared with the minute of flycatcher song stimulus ($t = 2.01$, $df = 17$, $P = 0.030$, one-tailed paired t-test) (cf. Fig. 6). Song rates, however, did not differ between intervals following least flycatcher song and control song intervals (Fig. 6).

In summary, least flycatchers presented with American redstart song moved closer to the song source (i.e., broadcast speaker). Such behavior would facilitate visual contact and thus attack of the redstart by the flycatcher. American redstarts presented with least flycatcher song reduced the frequency of flights immediately following song stimulus, when the risk of flycatcher attack may be greatest. Such behavior may reduce the risk of flycatcher attack on redstarts, with flycatchers apparently dependent on cues of redstart flight for visual recognition.

Our playback experiments demonstrate clearly the ability of least flycatchers and American redstarts to recognize and respond, with some specificity, to each other's song. Furthermore, these results illustrate the ability for these two species to recognize and respond to auditory stimuli extremely different from their own (Fig. 1A–C).

The marked differences in song morphology between the two species, as well as the flycatcher-specific response of redstarts, suggest heterospecific song recognition is an adaptive behavior and not simply misdirected intraspecific aggression. This differs from most cases of song recognition (in interspecifically territorial species), where response to heterospecific song is believed to be either misdirected (and nonadaptive) intraspecific aggression (Murray 1971, 1981), or to have originated in this manner (and be adaptive) (Cody 1969, 1974; Murray 1981).

The results of this experiment illustrate the capacity for interference competition to influence proximate behavior in the least flycatcher and American redstart. Sherry (1979) and Sherry and Holmes (1988) provide evidence for heterospecific effects on ecological strategies in these two species. There has been little attention paid, however, to heterospecific influences on aspects beyond food resource-related ecology. For example, characteristics of song and singing behavior of the redstart have always been examined from the perspective of intraspecific function (e.g., Lemon et al. 1985, 1987, 1993; MacNally and Lemon 1985). Similar effects of interspecific interference competition on other behavioral and ecological strategies, such as mating systems or intraspecific spacing, should be expected in these and other avian species (see e.g., Thornhill 1987, 1992).

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