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ORIGINAL ARTICLE

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Individual recognition of neighbors by song in a suboscine bird, the alder flycatcher *Empidonax alnorum*

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Abstract The ability of territorial males to discriminate between songs of their neighbors and songs of strangers has been demonstrated in 27 species of songbirds. Such experiments test only the ability of a subject to discriminate between two classes of stimuli, familiar (neighbors) and unfamiliar (strangers) songs. Individual recognition of neighbors is a finer, more complex type of discrimination. The ability of territorial males to recognize individual neighbors by song has been documented in 12 species of oscine passerines (Passeriformes, Passeri), but has never been demonstrated in suboscine passerines (Tyranni). We investigated recognition of songs of individual neighbors in a suboscine, the alder flycatcher (*Empidonax alnorum*). We performed a series of song playback experiments and recorded responses of territorial males to songs of neighbors and songs of strangers broadcast from two locations, the neighbor boundary and an opposite boundary. Subjects responded more aggressively to songs of a neighbor when played from the opposite boundary than when played from the neighbor boundary. They responded with equal aggression to songs of strangers regardless of location of playback. The difference in response to neighbor songs between speaker locations and the lack of a difference in response to stranger songs indicate that territorial males associate a particular song with a particular location (territory), and thus recognize individual neighbors.

Keywords Alder flycatchers · *Empidonax alnorum* · Individual recognition · Song · Suboscines

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Introduction

The avian order Passeriformes is divided into two suborders: Passeri (oscines) and Tyranni (suboscines). The order is monophyletic (Raikow 1982; Ericson et al. 2003) and suboscines assume the basal position within the clade (Ericson et al. 2003). Suboscines make up approximately 20% (1,151 species) of the order (Sibley and Monroe 1990), yet studies of bird song and its functions have focused almost exclusively on oscines. In a recent review (Catchpole and Slater 1995), only four studies dealing with suboscine song were cited.

The paucity of studies on suboscine song is surprising given that the two suborders apparently differ in mechanisms of song development. Learning and auditory feedback play a major role in the development of songs in all oscines studied (33 families; Kroodsma 1982). In contrast, vocal learning apparently is not required for development and production of normal song in suboscines (Kroodsma 1984). However, song ontogeny has only been studied in three suboscine species (Kroodsma 1984; Kroodsma and Konishi 1991). A potential effect of these different modes of song development may be greater individual variation in song structure in oscine species compared to most suboscines (Kroodsma 1996). Such variation might facilitate recognition of neighbors (Stoddard 1996).

The ability of territorial male oscines to discriminate between songs of neighbors and songs of strangers has been demonstrated experimentally in 27 species (reviews in: Falls 1982; Lambrechts and Dhondt 1995; Stoddard 1996). A territorial animal that possesses the ability to discriminate between neighbors (familiar) and strangers (unfamiliar) benefits by conserving energy as a consequence of avoiding unnecessary conflicts with familiar individuals. This differential treatment of neighbors and strangers by a territory owner has been termed the "dear enemy" effect (Fisher 1958).

Neighbor–stranger discrimination experiments test only the ability of a subject to discriminate between two classes of stimuli: neighbors (familiar) and strangers

Table 1 Published studies of individual recognition (*IR*) of neighbors by song in the order Passeriformes, arranged by family (according to American Ornithologists' Union 1998)

Family	Species	Common name	IR	IR speaker locations[a]	Stimuli presented[b]	References
Vireonidae	*Vireo olivaceus*	Red-eyed vireo	No	N, O	N	Godard 1993
Paridae	*Parus major*	Great tit	Yes	N, O	N, S	McGregor and Avery 1986
	Baeolophus bicolor	Tufted titmouse	No	N, O	N	Schroeder and Wiley 1983
Troglodytidae	*Campylorhynchus nuchalis*	Stripe-backed wren	Yes	N, O	N	Wiley and Wiley 1977
	Thryothorus pleurosticus	Banded wren	Yes	N	N	Molles and Vehrencamp 2001
Turdidae	*Erithacus rubecula*	European robin	Yes	N, O	N, S	Brindley 1991
	Luscinia luscinia	Thrush nightingale	Yes	N, O	N	Naguib and Todt 1998
Prunellidae	*Prunella modularis*	Dunnock	Yes	N, C	N, S	Langmore 1998
Motacillidae	*Anthus pratensis*	Meadow pipit	Yes	N, O	N	Elfström 1990
Parulidae	*Oporornis formosus*	Kentucky warbler	Yes	N, O	N	Godard and Wiley 1995
	Geothlypis trichas	Common yellowthroat	Yes	N, O	N, S	Wunderle 1978
	Wilsonia citrina	Hooded warbler	Yes	N, O	N	Godard and Wiley 1995
Emberizidae	*Melospiza melodia*	Song sparrow	Yes	N, C, O	N, S	Stoddard et al. 1991
	Zonotrichia albicollis	White-throated sparrow	Yes	N, C, O	N, S	Falls and Brooks 1975

[a] N neighbor boundary; C territory center; O opposite boundary
[b] N neighbor song; S stranger song

(unfamiliar). In a typical avian neighbor–stranger discrimination experiment, songs of a neighbor and songs of a stranger are broadcast sequentially from a speaker placed at the territory boundary shared by the subject and the neighbor. The rationale behind this experimental setup is that a territorial male views a neighbor singing from the territory boundary as less of a threat than a stranger singing from the same location. The territory holder should therefore respond weakly to the song of a neighbor in a familiar location, but strongly to the song of a stranger from the same location (Stoddard 1996).

Individual recognition is a finer, more complex type of discrimination (Axelrod and Hamilton 1981; Stoddard 1996). Individual recognition requires that the properties that are the basis for recognition be stereotyped within individuals, but differ sufficiently among individuals in a population, and that subjects in the population can detect these differences (Falls 1982).

Studies investigating individual recognition in birds have focused primarily on parent-offspring recognition (Beer 1970; Falls 1982; Beecher 1990) and mate recognition (Beer 1970; Falls 1982; Lampe and Slagsvold 1998; Wiley et al. 1991). Individual recognition of neighbors based on song differences has received relatively little attention, being documented in only 12 oscine species (Table 1; reviewed in: Falls 1982; Lambrechts and Dhondt 1995; Stoddard 1996). Acoustic recognition of individual neighbors also has been found in amphibians (e.g., Bee and Gerhardt 2002), fish (e.g., Myrberg and Riggo 1985; McGregor and Westby 1992), and mammals (e.g., Cheney and Seyfarth 1982).

Falls and Brooks (1975) were the first to demonstrate individual recognition of neighbors in a territorial songbird, the white-throated sparrow (*Zonotrichia albicollis*). They played songs of a neighbor and songs of a stranger sequentially from three locations: on the boundary shared by the subject and the neighbor, at the territory center of the subject, and on the territory boundary opposite the boundary shared with the neighbor. Subjects responded more strongly to stranger songs than to neighbor songs at the shared boundary and territory center. No difference in response was found between the two stimuli at the opposite boundary. These results suggest that male white-throated sparrows can recognize the songs of individual neighbors. However, only one subsequent study has used the three-location methodology (Stoddard et al. 1991; Table 1). Eleven other studies have tested responses to playback of songs of neighbors at only two locations, either the boundary shared by the subject and the neighbor (neighbor boundary) and the territory boundary opposite the neighbor boundary (opposite boundary), or the neighbor boundary and at the territory center (Table 1). The rationale behind these latter designs is that a neighbor would sing at the opposite boundary or territory center only if he were shifting or expanding his territory, or trying to usurp the territory of the subject (Stoddard 1996). The differential response to neighbor songs from the two locations suggests that subjects associate a particular song with a particular location, a type of individual recognition (Stoddard 1996). In 9 of the 11 studies that used the two-location design to test individual recognition of neighbors, subjects responded more strongly when neighbor songs were played from the opposite boundary or territory center than when they were played from the neighbor boundary. In the two studies that found no individual recognition ability (Table 1), the authors suggested that the subjects had song features that made discrimination difficult or that they viewed their neighbors as equally threatening as a stranger (Schroeder and Wiley 1983; Godard 1993). In addition to differences in the number of speaker locations used, previous studies have also varied in the number of stimuli presented to subjects. Eight of the 14 studies used only songs of neighbors broadcast at all speaker locations, while 6 studies used both songs of neighbors and strangers broadcast at all speaker locations (Table 1). Wiley and Wiley (1977) and Stoddard (1996) advocated using the latter method, suggesting it was "more powerful" than simply playing a single stimulus. Those studies that failed to demonstrate

individual recognition of neighbors used the simpler design.

We know almost nothing about song recognition in the suboscine passerines (Stoddard 1996). The limited individual variation in suboscine songs raises questions regarding the ability of suboscines to recognize individual neighbors by song. Our objective was to determine whether a suboscine, the alder flycatcher (*Empidonax alnorum*), could use inter-individual variation in songs to recognize individual neighbors. The alder flycatcher has a single, relatively simple song type, described verbally as 'fee-bee-o' (Stein 1963). In addition to the 'fee-bee-o' song, the alder flycatcher produces a variety of non-song vocalizations (Stein 1963). These include 'zwee-oo', double-peak, 'wee-oo', 'pit', and 'churr' calls notes (see Fig. 2 in Lovell and Lein 2004a). With the exception of the 'pit' call, use of these calls is restricted almost completely to aggressive interactions. Previous analyses demonstrated limited variation of song features within individual males in a population in western Alberta, but sufficient variation among males to permit statistical identification of songs of individuals (see Fig. 2 in Lovell and Lein 2004b). This suggests that there is sufficient variation among males to permit individual recognition of territorial neighbors.

Song playback experiments showed that territorial males could discriminate between songs of neighbors and strangers (Lovell and Lein 2004a). The current study examined whether alder flycatchers are capable of recognizing the songs of individual territorial neighbors, as opposed to discriminating between familiar and unfamiliar songs. Our null hypothesis was that alder flycatchers would not recognize individuals by their songs. If alder flycatchers can recognize individuals, we predict that: (1) they would demonstrate different responses to songs of neighbors played from the neighbor and opposite boundaries, with a more aggressive response directed toward songs broadcast from the opposite boundary; and (2) they would not respond differently to songs of strangers at the two locations.

Methods

Study site

We worked at Bryant Creek (51°02′N, 114°47′W), in the Rocky Mountain foothills approximately 80 km west of Calgary, Alberta, Canada (Lovell and Lein 2004a). During the breeding season of 2002, we captured four males, banded them, and marked them with hair dye on their breasts for identification. Two additional males that were banded in 2001 returned to Bryant Creek in 2002. Unmarked individuals (n=14) were identified by territory position and persistent use of specific song perches. We confirmed identifications by tape-recording songs of subjects or neighbors on the day preceding the experiment and comparing audiospectrograms to previous recordings of birds in those territories (Lovell and Lein 2004a, 2004b). Territory boundaries were determined from the location of song perches combined with a modified version of the "flush method" (Reed 1985).

Song recordings and stimuli construction

We recorded songs with Nagra 4.2 or Stellavox SR-8 reel-to-reel tape recorders and either a Sennheiser K6-P microphone in a Telinga parabolic reflector or a Telinga Pro II parabolic microphone. Digital sound files of songs were acquired from tapes at a sample rate of 25 kHz using RTSD Ver. 1.10 bioacoustical software (Engineering Design, Belmont, Mass.). Playback stimuli were made using SIGNAL Ver. 4.0 bioacoustical software (Engineering Design). Each stimulus sound file was 3 min long, with a 'fee-bee-o' song every 5 s, matching the normal song rate (12 songs/min). We burned stimulus files onto Kodak CD-R Ultra 80 compact discs for playback. Details of the protocol for selection and preparation of stimulus songs are given elsewhere (Lovell and Lein 2004a).

Design of playback experiments

We performed two sets of experiments with the same protocol, one set to test responses to neighbor songs and one set to test responses to stranger songs. Each experiment presented a single stimulus (a neighbor song or a stranger song) sequentially at two speaker locations (the neighbor and opposite boundaries). A neighbor was an individual with a territory bordering that of the subject, while a stranger had a territory over six territory diameters (> 1 km) away from the subject. Speaker locations were defined relative to the subject of the experiment. The neighbor boundary was the territory boundary shared by the subject and the neighbor whose song was used, and the opposite boundary was the territory boundary of the subject opposite the neighbor boundary.

To avoid pseudoreplication, we used ten unique neighbor songs as stimuli for ten subjects in neighbor song experiments and ten different stranger songs as stimuli for ten subjects in stranger song experiments (Kroodsma 1989). In both sets of experiments, we randomized initial speaker location (neighbor boundary or opposite boundary) to control for any effect of order of presentation, but were unaware of which stimulus was being broadcast while conducting individual experiments. Thus the experiments were conducted blindly, reducing possible observer bias.

We conducted experiments from 28 June to 23 July 2002, between 0500 and 1000 hours (MST), to minimize any effects of date or time of day on responses. Subjects and their neighbors were in various stages of the breeding cycle (from nest-building to fledgling stages) when tested for individual recognition. Because we could not accurately determine the breeding stage of each subject during the experiments, we used date of the trial as a substitute measurement (Lovell and Lein 2004a).

Each trial lasted 9 min. During the first 3 min, we played a 'fee-bee-o' song through a Bose Model 151 speaker connected to a Sony D-E351S portable CD player. The speaker was located within 5 m of the boundary and approximately 2 m above the ground, and facing into the territory of the subject. The speaker was mounted in front of a parabolic reflector (Molles and Vehrencamp 2001) lined with foam to reduce neighbor interference. We matched playback volume to that of a naturally-singing bird (68–71 dB at 3 m from the speaker, measured with a Radio Shack Model 33–2055 sound level meter set at "C" weighting and fast response). The final 6 min of each trial recorded how the subject behaved once the stimulus had ceased.

To avoid habituation to speaker location, non-independence of trials, and biased responses to playback, subjects on adjacent territories were not tested on the same day. In preliminary experiments we determined that intervals of 30–60 min between trials (typical of many individual recognition experiments) were insufficient to allow birds to return to pre-stimulus levels of behavior. Therefore, we waited 24 h between trials on individual subjects. Experiments began only after both the subject and its neighbor had been silent for >5 min. No experiments proceeded under conditions of heavy rain or winds 20 km/h.

Table 2 Responses to neighbor song (*NS*) and stranger song (*SS*) stimuli recorded during experiments testing individual recognition of neighbor songs by alder flycatchers (*Empidonax alnorum*). Songs were broadcast from the neighbor boundary (*NB*) and the opposite boundary (*OB*). All values given as mean±SE

	NS stimulus		SS stimulus	
Response measure[a]	NB	OB	NB	OB
Latency to first approach within 10 m (s)	69.1±38.1	244.3±65.0	219.6±72.1	231.6±77.8
Closest approach to speaker (m)	1.1±0.7	2.0±0.5	1.5±0.5	1.4±0.6
Latency to first flight toward speaker (s)	243.8±70.9	385.9±45.5	417.1±30.8	422.1±38.3
Total time within 10 m of speaker (s)	9.6±7.4	98.2±39.9	94.1±34.9	92.4±42.5
Number of flights	2.8±1.1	5.5±1.3	6.8±1.8	6.9±1.4
Latency to first call note vocalization (s)	434.7±36.4	519.0±11.5	439.6±43.9	450.1±51.6
Total number of call notes	36.6±11.9	86.3±27.5	83.6±19.8	80.9±26.9
Number of 'fee-bee-o' songs	22.7±13.2	8.9±4.1	7.2±4.8	8.0±3.9
Latency to first 'fee-bee-o' song (s)	178.5±66.4	138.5±68.2	235.2±74.0	243.7±81.7

[a] Latency and closest approach variables were transformed by subtracting the original values from maximum possible values (540 s and 10 m respectively) so that larger values indicated a strong response

Data collection and statistical analysis

Two observers used cassette tape-recorders to record vocalizations and locations of subjects during experiments. We extracted 17 response measures from these behavioral descriptions and vocalization tapes using EthoLog 2.25 software (Ottoni 2000), including measures of singing behavior, vocalization, approach to the speaker, and latencies of response (Appendix 1). These were reduced to nine prior to analysis (Table 1). The frequency and latency of 'pit' call notes were omitted because this is primarily a location vocalization given between males and females. The double-peak, 'wee-oo', 'churr', and 'zwee-oo' call notes were often given in series, indicating that these individual call notes have similar meanings. Therefore, they were combined into a single response measure, total number of call notes, for subsequent analyses. The latencies of individual call note vocalizations were combined into a single response measure, latency to first call note vocalization.

We used SYSTAT 10.2 software (SPSS, Chicago, Ill.) for all statistical analyses. We transformed latency and closest approach variables by subtracting original values from maximum possible values (540 s and 10 m respectively) so that larger values indicated stronger responses (McGregor 1992). Separate data sets were generated for neighbor song experiments and for stranger song experiments. To reduce the number of variables and to eliminate problems caused by colinearity of variables, we performed a principal components analysis (PCA) on each data set (McGregor 1992). ANOVAs analyzing the possible effect of order of stimulus presentation on principal component (PC) scores were conducted. We conducted regression analyses to determine if time of day or date had significant effects on responses as measured by PC scores.

Loadings of original variables on each PC were examined to interpret their biological meanings. We used two MANOVAs to test for differences in PC scores between responses at the two speaker locations for neighbor songs and for stranger songs, respectively. To determine which response measures contributed to differences in responses at the two speaker locations, we conducted ANOVAs on scores on each PC from each data set. We predicted that subjects would respond to the songs of neighbors broadcast from the opposite boundary more aggressively than songs of neighbors broadcast from the neighbor boundary. Because we predicted a directional difference in responses to songs on neighbors, we used one-tailed probabilities in both the MANOVA and ANOVAs in the neighbor song trials. We did not predict a directional difference in responses to songs of strangers, and therefore used two-tailed probabilities in both the MANOVA and ANOVAs in the stranger song trials.

Results

Experiments with songs of neighbors

We completed ten experiments. Seven of nine variables showed higher values for responses to songs of a neighbor when broadcast from the opposite boundary than when played from the neighbor boundary (Table 2). The only exceptions were number of 'fee-bee-o' songs and latency to first 'fee-bee-o' song (Table 2). Alder flycatchers responded to songs of neighbors broadcast from the two locations with different patterns of behavior. Subjects responded to songs played from the opposite boundary by approaching the speaker quickly, vocalizing with call notes, and actively searching for the intruder, often flying back and forth over the speaker (Table 2). However, when songs were played from the neighbor boundary, subjects often did not approach the speaker and just vocalized with 'fee-bee-o' songs (Table 2). Alder flycatchers spent an average of 10 times longer within 10 m of the speaker in response to songs from the opposite boundary than in response to songs from the neighbor boundary (Table 2). Songs broadcast from the opposite boundary elicited an average of 2.5 times as many call notes per trial than did songs played from the neighbor boundary (Table 2). However, alder flycatchers responded to songs from the neighbor boundary by giving almost 3 times as many 'fee-bee-o' songs as they did in response to songs from the opposite boundary (Table 2).

PCA generated three PCs with eigenvalues >1.0 that explained approximately 73% of the variance in the response variables. Order of stimulus presentation had no effect on strength of response (ANOVAs on scores on three PCs: all $F_{1,18}<1.34$; all $P>0.262$). Regression analyses of scores on the three PCs on time of day and date of the experiment showed no significant influences on the strength of response (time of day: all $r^2<0.099$, all $F_{1,18}<3.09$, all $P>0.139$; date: all $r^2<0.111$, all $F_{1,18}< 3.38$, all $P>0.083$).

Five of the response measures that had medium-sized to high correlations ($r>0.4$) with PC1 were approach response measurements (Table 3). We thus interpret PC1 as an approach response to playback. Three vocal response measures had medium-sized to high correlations with PC2

Table 3 Factor loadings for the nine response variables on the three principal components for neighbor song trials in playback experiments testing individual recognition of neighbor songs by alder flycatchers. Loadings with r>=0.4 are shown in bold face

Response measures	Factor loadings		
	PC1	PC2	PC3
Number of flights	**0.862**	0.312	0.099
Latency to first approach within 10 m	**0.861**	0.003	–0.281
Latency to first flight toward speaker	**0.781**	0.071	0.211
Total time within 10 m of speaker	**0.692**	–0.212	**–0.507**
Closest approach to speaker	**0.659**	**–0.439**	–0.104
Latency to first 'fee-bee-o' song	0.134	**0.809**	0.199
Number of 'fee-bee-o' songs	0.234	**0.801**	0.180
Total number of call notes	0.131	**–0.455**	**0.732**
Latency to first call note vocalization	**0.428**	–0.294	**0.577**
% variance explained	36.45	21.43	14.91

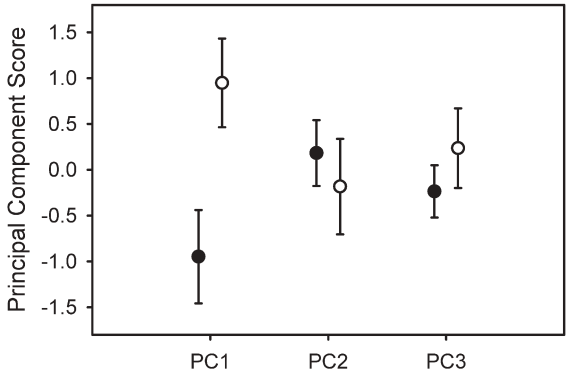

Fig. 1 Mean scores (±SE) on the first three principal components for responses to neighbor songs broadcast from the neighbor (*filled circles*) and opposite territory boundaries (*open circles*) of subjects

and two vocal response measures that had medium-sized to high correlations with PC3 (Table 3). We interpret both PC2 and PC3 as vocal responses to song playback (Table 3).

A one-tailed MANOVA conducted on the scores on the three PCs showed a significant difference between responses to neighbor stimuli broadcast from the two locations ($F_{3,16}$=2.873, P=0.034). Scores on PC1 differed significantly between speaker locations (one-tailed ANOVA on PC1: $F_{1,18}$=7.291, P=0.007; Fig. 1). There were no significant differences in PC2 and PC3 scores (one-tailed ANOVA on PC2: $F_{1,18}$=0.334; P=0.285; PC3: $F_{1,18}$=0.820, P=0.189; Fig. 1).

Experiments with songs of strangers

We completed ten experiments. All nine response measures show equivalent responses to songs of strangers at both song broadcast locations (Table 2).

PCA generated four principal components with eigenvalues >1.0, explaining approximately 79% of the variance in the response variables. Order of stimulus presentation had no effect on strength of response (ANOVAs on scores on four PCs: all $F_{1,18}$<0.604 ; all P>0.447). Regression analyses of scores on the four PCs on time of day and date of the experiment showed no significant influences on the strength of response (time of day: all r^2<0.005, all $F_{1,18}$<1.09, all P>0.311; date: all r^2<0.087, all $F_{1,18}$<2.18, all P>0.111).

Seven of the variables had medium-sized to high correlations (r>0.4) with PC1 (Table 4); the only exceptions were the two response measurements involving flight (Table 4). Six of the vocal and approach response measures had medium-sized to high correlations with PC2 (Table 4). We interpret PC1 and PC2 as measures of both approach and vocal response to playback (Table 4). Number of flights and latency to first flight had medium-sized to high correlations with PC3 (Table 4). PC3 was thus interpreted as an approach response to playback. Number of call notes and number of 'fee-bee-o' songs had medium-sized to high correlations with PC4 (Table 4) and we interpret it as a vocal response (Table 4).

A two-tailed MANOVA conducted on the scores on the four PCs showed no significant influence of speaker location on responses ($F_{4,15}$=0.036, P=0.997). Scores on the four PCs did not differ significantly between speaker

Table 4 Factor loadings for the nine response variables on the four principal components for stranger song trials in playback experiments testing individual recognition of neighbor songs by alder flycatchers. Loadings with r>=0.4 are shown in bold face

Response measures	Factor loadings			
	PC1	PC2	PC3	PC4
Latency to first approach within 10 m	**0.776**	**0.531**	0.165	–0.119
Latency to first 'fee-bee-o' song	**0.690**	**–0.544**	0.081	0.156
Closest approach to speaker	**0.586**	**0.480**	-0.065	–0.324
Total time within 10 m of speaker	**0.575**	**0.484**	**0.443**	0.147
Latency to first call note vocalization	**0.418**	**–0.624**	0.106	–0.327
Total number of call notes	**0.453**	**–0.511**	–0.262	**–0.464**
Number of flights	0.332	0.184	**–0.837**	0.058
Latency to first flight toward speaker	0.263	0.044	**–0.712**	**0.429**
Number of 'fee-bee-o' songs	**0.475**	–0.372	0.293	**0.641**
% variance explained	28.19	20.74	17.87	12.07

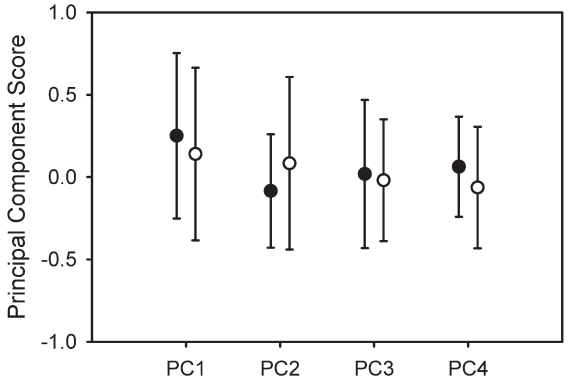

Fig. 2 Mean scores (±SE) on the first four principal components for responses to stranger songs broadcast from the neighbor (*filled circles*) and opposite territory boundaries (*open circles*) of subjects

locations (two-tailed ANOVA on PC1: $F_{1,18}$=0.023, P=0.880; PC2: $F_{1,18}$=0.071; P=0.792; PC3: $F_{1,18}$=0.004, P=0.950; PC4: $F_{1,18}$=0.069, P=0.795; Fig. 2).

Discussion

Despite a mode of song development that does not involve learning, and the relatively limited variation in their songs, alder flycatchers display the same type of ability to recognize individual neighbors as found in the 12 oscine species in which this phenomenon has been documented. Subjects responded to songs of neighbors broadcast from the opposite boundary by flying toward the speaker more quickly, spending more time within 10 m of the speaker, and by vocalizing more quickly and more often with call notes than when responding to songs of neighbors broadcast from the neighbor boundary. This differential reaction at the two speaker locations suggests a more aggressive response at the opposite boundary. A closer, quicker approach to the speaker may signal that an individual is willing to fight (Stoddard 1996). Additionally, a high number call note vocalizations may reflect a more aggressive response compared to a high number of 'fee-bee-o' songs. In natural aggressive encounters between males, alder flycatchers vocalize almost exclusively with call notes and rarely with 'fee-bee-o' songs (Lovell personal observation). By vocalizing more with 'fee-bee-o' songs than with call notes, subjects were responding with a lower level of aggression to the neighbor stimuli from the neighbor boundary (Lovell and Lein 2004a).

Responses to stranger songs broadcast at either location resemble responses to neighbor songs at the opposite boundary. Subjects responded by flying toward the speaker, spending most of the trial within 10 m of the speaker, and by vocalizing with almost exclusively with call notes. This suggests that alder flycatchers may view a neighbor singing from the incorrect location and a stranger as equally threatening.

Recently, the methodology for testing individual recognition of neighbors has been questioned (e.g., Bee and Gerhardt 2002; Husak and Fox 2003). These authors argue that simply testing responses of a subject to stimuli presented at the neighbor and opposite boundaries does not test individual recognition adequately. Bee and Gerhardt (2002) suggested that this experimental design is flawed because it does not take in to account location dependence as a possible confounding variable. They also argued that location dependence contradicts Falls' (1982, p. 238) definition of individual recognition as "discrimination among similar sounds of different individuals in the absence of other identifying cues", and that location may act as an identifying cue that aids in individual recognition of neighbors. Husak and Fox (2003) made a similar argument, suggesting that "environmental context" may be necessary for individual recognition of neighbors. In other words, a neighbor out of its normal location may be viewed by a subject as simply another stranger. However, these concerns are about the proximate mechanisms of individual recognition and do not invalidate the results of previous experiments of individual recognition of neighbors. Subjects in these individual recognition experiments demonstrated differential responses to the songs of neighbors presented at different locations. Subjects were not responding solely to the specific song, nor were they responding solely to the location at which that song was presented. Rather, they were responding to that specific song at that specific location, a form of individual recognition (Stoddard 1996).

Our results therefore meet both of the requirements for demonstration of individual recognition of neighbors. As predicted, subjects responded more aggressively to songs of neighbors played from the opposite territory boundary than to songs of neighbors played from the neighbor boundary (Fig. 1) and subjects responded with equal aggression to the songs of a stranger played from the two locations (Fig. 2). The differential response to neighbor songs indicates that alder flycatchers are not simply habituated to a familiar song, but associate a specific song with a specific location. This causes us to reject our null hypothesis that alder flycatchers would not recognize individuals by their songs.

Alder flycatchers may benefit from individual recognition of neighbors by being able to assess the relative threat that an individual neighbor presents and respond accordingly (Stoddard 1996). Additionally, there might be other benefits to recognizing neighbors, such as enhanced breeding success in the presence of familiar neighbors compared to breeding success in the presence of unfamiliar neighbors. Territorial male red-winged blackbirds (*Agelaius phoeniceus*) with familiar neighbors fledged more offspring and had larger harem sizes than did territorial males with unfamiliar neighbors (Beletsky and Orians 1989).

Song and its functions have been neglected in suboscines. Our study is the first to test for the ability to recognize individual neighbors by song in a suboscine. Only seven other studies have investigated song function in suboscines experimentally (Smith 1988; Smith and Smith 1992, 1996; Morton and Derrickson 1996; Westcott

1997; Bard et al. 2002; Lovell and Lein 2004a). We hope that our findings will stimulate additional research on the structure and function of song in more suboscine species

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Appendix

Table 5 lists response measures recorded during song playback experiments

Table 5 Seventeen response measures recorded during song playback experiments testing individual recognition of neighbors by song by alder flycatchers.

Response measure
Latency to first approach within 10 m (s)
Closest approach to speaker (m)
Latency to first flight toward speaker (s)
Total time within 10 m of speaker (s)
Number of flights
Number of 'pit' call notes
Latency to first 'pit' call note (s)
Number of 'fee-bee-o' songs
Latency to first 'fee-bee-o' song (s)
Number of double-peak call notes
Latency to first double-peak call note (s)
Number of 'zwee-oo' call notes
Latency to first 'zwee-oo' call note (s)
Number of 'churr' call notes
Latency to first 'churr' call note (s)
Number of 'wee-oo' call notes
Latency to first 'wee-oo' call note (s)

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