Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*

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Bird song and its functions have been studied extensively for more than 50 years, but almost entirely in oscine passerines. Few studies have investigated any aspect of song in suboscine passerines. This is significant because song development and the extent of individual variation in song differs greatly between these groups. Learning and auditory feedback play major roles in song development in all oscines studied, but apparently no part in song ontogeny in suboscines. The ability of territorial oscine males to discriminate between songs of neighbors and strangers has received considerable attention, but this phenomenon is virtually unstudied in suboscines. We tested whether a suboscine bird, the alder flycatcher (*Empidonax alnorum*), was able to discriminate between songs of neighbors and strangers despite limited individual variation in song. We performed playback experiments to measure responses of males to songs of neighbors and strangers broadcast from the territory boundary shared by the subject and the neighbor. Subjects responded more aggressively to songs of strangers than to songs of neighbors. These results further our understanding of the evolution of song and its functions in suboscines by demonstrating that, similar to their oscine relatives, they can discriminate between the songs of neighbors and strangers. *Key words:* alder flycatchers, *Empidonax alnorum*, neighbor-stranger discrimination, song, suboscine, territoriality. *[Behav Ecol 15:799–804 (2004)]*

Many territorial animals display lower levels of aggression toward familiar neighbors than toward unfamiliar strangers (for review, see Temeles, 1994), a phenomenon termed the "dear enemy" effect (Fisher, 1958). Neighbor-stranger discrimination (hereafter NSD) has been documented in a variety of animal taxa, including insects (see Gordon, 1989; Thomas et al., 1999), amphibians (see Bee and Gerhardt, 2001), fish (see McGregor and Westby, 1992), reptiles (see Whiting, 1999), and mammals (see Rosell and Bjørkøyli, 2002). However, most studies of NSD have dealt with territorial songbirds (for review, see Stoddard, 1996). Although other taxa use various sensory cues to discriminate neighbors from strangers, including calls and mechanical sounds (see Bee and Gerhardt, 2001; Randall, 1994), visual cues (see Whiting, 1999), or chemical and olfactory cues (see Thomas et al., 1999), songbirds rely on complex vocalizations (songs) as the cue.

The discriminatory cues used for NSD vary across taxa, but the value of discriminating neighbors from strangers appears to be similar. Excessive expenditure of time and energy in territorial defense may reduce the fitness of a territory holder. By avoiding unnecessary conflicts with familiar individuals, a territorial animal that possesses the ability to discriminate between neighbors (familiar) and strangers (unfamiliar) may benefit by conserving energy. Familiar individuals already maintain and defend territories of their own, thus presenting little threat to the territory holder. However, unfamiliar individuals could be intruders looking for a territory, thus constituting a stronger potential threat (Stoddard, 1996).

Studies of avian NSD have used song playback experiments that simulate interactions of a territorial bird with its neighbor or a stranger. The rationale is that a territorial male views a song of a neighbor broadcast from the territory boundary as less of a threat than a song of a stranger heard from the same location. Therefore, the territory holder should 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). NSD has been tested in 27 oscine passerines (order Passeriformes, suborder Passeri; for reviews, see Falls, 1982; Lambrechts and Dhondt, 1995; Stoddard, 1996). All but one study found that subjects could discriminate between songs of conspecific neighbors and strangers. In the case in which no NSD was found, the investigators suggested that the subjects had song features that made discrimination difficult (Falls and d'Agincourt, 1981).

Suboscine passerines (suborder Tyranni) make up approximately 20% (1151 species) of the order Passeriformes and are a dominant part of Neotropical avifaunas (Sibley and Monroe, 1990). Despite the predominance of suboscines in the Neotropics, our knowledge of bird song and its functions is biased heavily toward studies of oscines. Of 418 papers on passerine song cited in a recent review (Catchpole and Slater, 1995), only four dealt with suboscines. The lack of studies on suboscine song is significant 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, although song development has been examined in only three suboscine species (Kroodsma, 1984; Kroodsma and Konishi, 1991). A possible effect of these different modes of song development may be greater individual variation in song structure exhibited by oscines in comparison to most suboscines (Kroodsma, 1996). Such variation might facilitate recognition of neighbors (Stoddard, 1996). The limited variation in suboscine songs raises questions regarding their ability to discriminate between songs of neighbors and strangers. We know almost nothing about song discrimination in suboscines (Stoddard, 1996).

Our objective was to determine whether a suboscine, the alder flycatcher (*Empidonax alnorum*), could use inter-individual variation in songs to distinguish between songs of neighbors and songs of strangers. The alder flycatcher has one relatively simple song type, described verbally as "fee-bee-o" (Stein,
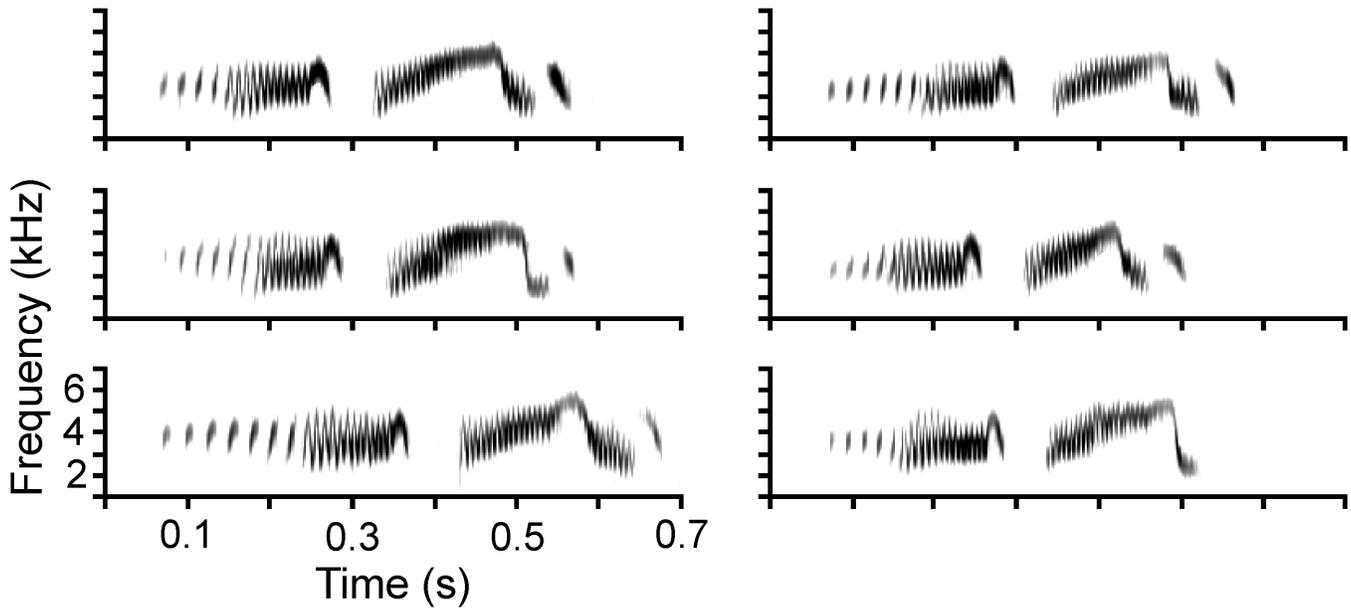
Figure 1
Audiospectrograms of fee-bee-o songs of six individual alder flycatchers, indicating variation among individuals.

1963) (Figure 1). It is one of the three suboscines in which song development has been examined (Kroodsma, 1984). Individual variation is a prerequisite for NSD by song (Falls, 1982). We demonstrated sufficient stereotypy of song features within males, and sufficient variation among males, in a population of alder flycatchers in western Alberta to permit statistical identification of songs of individuals (Lovell and Lein, 2004) (Figure 1). This suggests that there is sufficient variation among males to permit individual recognition of territorial neighbors by the birds. In addition to the fee-bee-o song, the alder flycatcher produces a variety of nonsong vocalizations (Stein, 1963). These include "zwee-oo," double-peak, "wee-oo," "pit," and "churr" calls notes (Figure 2). With the exception of the pit call, use of these calls is restricted almost completely to aggressive interactions.

Our null hypothesis was that alder flycatchers would not discriminate between songs of neighbors and strangers. If alder flycatchers can discriminate between songs of neighbors and strangers, then a more aggressive response directed toward the song of strangers is predicted.

METHODS

Our study was conducted at Bryant Creek (51°02′ N, 114°47′ W), located in the Rocky Mountain foothills approximately 80 km west of Calgary, Alberta, Canada. Alder flycatchers breed in willow (*Salix* spp.) and bog birch (*Betula glandulosa*) thickets bordering streams and beaver ponds. During the breeding season of 2002, four males were captured by using mist nets, banded, and marked with hair dye on their breasts for identification. In addition, two males that were banded in 2001 returned to Bryant Creek in 2002. Unmarked individuals ($n = 20$) were identified by territory position and persistent use of specific song perches. To confirm identifications, we
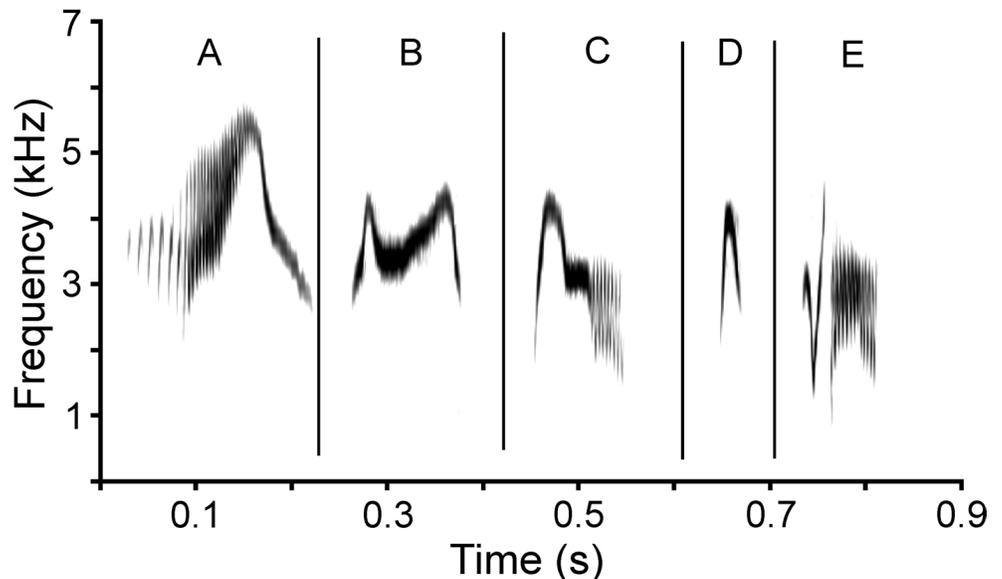
Figure 2
Audiospectrograms of call notes of alder flycatchers. (A) Zwee-oo call note. (B) Double-peak call note. (C) Wee-oo call note. (D) Pit call note. (E) Churr call note. Vertical lines indicate discontinuities in the time axis.

tape-recorded all males chosen as subjects or neighbors in experiments on the day before the experiment and compared audiospectrograms of their songs to previous recordings of birds in those territories. This procedure was possible because alder flycatchers have individually distinctive songs (Lovell and Lein, 2004) (Figure 1). We determined territory boundaries by using the location of song perches combined with a modified version of the "flush method" (Reed, 1985).

Songs were recorded 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 the tapes at a sample rate of 25 kHz by using RTSD version 1.10 bioacoustical software (Engineering Design) with a Gateway 2000 P5-166 desktop computer and a DT-2821G I/O board for analog-to-digital conversion. During acquisition, analog input signals were processed through a Krohn-Hite Model 3550 filter to eliminate aliasing.

We viewed audiospectrograms of stimulus songs with RTSD to insure that they were free of background noise in the frequency range of alder flycatcher song. Playback stimuli were made by using SIGNAL version 4.0 bioacoustical software (Engineering Design). We normalized the amplitude of stimulus songs and digitally filtered them by using a band-pass filter set between 1 kHz and 8 kHz to remove low- and high-frequency background noise. We then resampled each stimulus song at 44.1 kHz (CD quality) and concatenated them (CONCAT function in SIGNAL) to produce a stimulus sound file 3 min long, with a fee-bee-o song every 5 s. This matched the normal song rate of an alder flycatcher (12 songs/min). We burned stimulus files onto Kodak CD-R Ultra 80 compact discs for playback.

Each experiment consisted of two trials, one presenting songs of a neighbor and one presenting songs of a stranger. A neighbor was an individual with a territory bordering that of the subject, whereas a stranger had a territory more than six territory diameters (more than 1 km) away from the subject. We used 26 unique neighbor songs as stimuli for 26 subjects, avoiding pseudoreplication (Kroodsma, 1989). We used 26 different songs as stranger stimuli for 26 subjects. Twelve stimuli used as neighbor songs were also used as stranger songs in other experiments. The other 14 stranger songs were recorded during 2002 at two locations 8–10 km from Bryant Creek. We randomized the order of trials for each subject to control for any effect of order of presentation, but were unaware of the order of presentation while conducting individual experiments. Thus, the experiments were conducted blindly, reducing possible observer bias.

We conducted experiments from 23 June–19 July 2002, between 0500 and 1000 h (mountain standard time), 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 NSD. Because we could not determine the breeding stage of each subject during the experiments, we used date of the trial as a substitute. This is logical given the short breeding season (less than 60 days) and high degree of reproductive synchrony (most males were paired within 2–3 days after the first arrival of females; Lovell SF, unpublished data).

Each trial lasted 9 min (3 min of playback and 6 min of silence). During the first 3 min, a fee-bee-o song was broadcast through a Bose Model 151 speaker connected to a Sony D-E351S portable CD player. We placed the speaker within 5 m of the boundary shared by the subject and the neighbor, 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, which was

Table 1

Response measures recorded during neighbor-stranger discrimination experiments on alder flycatchers

Response measure	Neighbor stimulus	Stranger stimulus
Latency to first approach within 10 m (s)	180.2 ± 41.8	249.8 ± 39.0
Closest approach to speaker (m)	1.9 ± 0.5	3.1 ± 0.6
Latency to first flight toward speaker (s)	341.7 ± 34.9	400.9 ± 19.1
Total time within 10 m of speaker (s)	86.0 ± 25.8	122.9 ± 27.7
Number of flights	4.4 ± 0.6	6.2 ± 0.6
Latency to first vocalization (s)	453.1 ± 22.4	428.3 ± 27.7
Total number of call notes	23.8 ± 5.2	46.2 ± 7.9
Number of fee-bee-o songs	21.6 ± 5.5	12.1 ± 3.6

Values are mean ± SE. 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 indicate a stronger response.

a serious problem in preliminary trials. Volume of song playback was matched 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 remaining 6 min of each trial recorded how the subject behaved once the stimulus had ceased.

To avoid problems such as habituation to speaker location, nonindependence of trials, and biased responses to playback, subject males on adjacent territories were not tested on the same day. Preliminary experiments indicated that intervals of 30–60 min between trials (typical of many NSD experiments) were not sufficient to allow birds to return to prestimulus levels of behavior. Therefore, we waited 24 h before presentation of the second stimulus to individual subjects. All playback experiments began only after both the subject and its neighbor had been silent for more than 5 min. Timing of trials started at the beginning of the first fee-bee-o song of the playback. No experiments proceeded under conditions of heavy rain or winds 20 km/h or more.

Two observers used cassette tape-recorders to record vocalizations and locations of subjects during experiments. We transcribed these behavioral description and vocalization tapes by using EthoLog 2.25 software (Ottoni, 2000). The 17 response measures we recorded during each trial were similar to those used in previous playback experiments (Brindley, 1991), and included measures of singing behavior, vocalization, approach to the speaker, and latencies of response (Appendix). These were reduced to eight before analysis (Table 1). The original measurements included counts and latencies to first vocalization for each call note type. 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 vocalizations (call notes or song) were combined into a single response measure, latency to first vocalization.

SYSTAT 10.2 software (SPSS Inc.) was used in all statistical analyses. Latency and closest approach variables were transformed by subtracting original values from maximum possible values (540 s and 10 m, respectively) so that larger values indicated a stronger response (McGregor, 1992). Some response measures were highly correlated. Therefore, we

Table 2

Factor loadings on the three principal components for the eight response variables in neighbor-stranger discrimination experiments with alder flycatchers

Response measures	Factor loadings		
	PC1	PC2	PC3
Latency to first approach within 10 m	**0.897**	−0.219	0.077
Closest approach to speaker	**0.820**	−0.199	−0.123
Latency to first flight toward speaker	**0.750**	0.289	0.086
Total time within 10 m of speaker	**0.737**	**−0.478**	0.042
Number of flights	**0.634**	**0.542**	−0.147
Latency to first vocalization	0.083	**0.778**	0.130
Total number of call notes	0.080	**0.545**	**−0.685**
Number of fee-bee-o songs	0.097	**0.443**	**0.767**

Loadings $r > |0.4|$ are shown in boldface.

performed a principal components analysis (PCA) to reduce the number of variables and to eliminate problems caused by colinearity (McGregor, 1992). ANOVAs analyzing the effect of order of stimulus presentation on principal components (PC) scores were conducted. Regression analyses were conducted to determine if time of day or date had significant effects on responses as measured by PC scores.

We examined component loadings to interpret the biological meaning of each PC. We used a MANOVA to test for differences in PC scores between neighbor and stranger trials. To determine which response measures contributed to differences in responses to songs of neighbors and to songs of strangers, we then conducted an ANOVA on scores on each PC.

RESULTS

We completed a total of 26 experiments successfully. Subjects typically responded to playback of all song stimuli by flying toward the speaker and beginning to vocalize, usually with a fee-bee-o song.

Six of the eight variables show higher values for responses to songs of strangers than to songs of neighbors (Table 1). The two exceptions were latency to first vocalization and number of fee-bee-o songs (Table 1). Alder flycatchers responded to songs of neighbors and songs of strangers with different patterns of behavior. They responded to songs of strangers by approaching the speaker quickly, actively searching for the intruder within 10 m of the speaker, and vocalizing mainly with aggressive call notes (Table 1). However, when songs of neighbors were broadcast, they often failed to approach within 10 m of the speaker, opting instead to stay where they were and vocalize more quickly, using fee-bee-o songs (Table 1).

PCA generated three PCs with eigenvalues greater than 1.0, explaining approximately 74% 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 $F_{1,50} < 2.35$; all $p > .131$). 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 $r^2 < .024$, all $p > .139$; date: all $r^2 < .020$, all $p > .162$).

Five of the variables with high correlations ($r > |0.4|$) with PC1 were approach measurements (Table 2), and we interpret PC1 as an approach response to playback. Three vocal response measures had high correlations with PC2, and two vocal response measures had high correlations with PC3 (Table 2). We interpret PC2 and PC3 as vocal responses to playback.

A one-tailed MANOVA conducted on the scores on the three PCs showed a highly significant difference between responses to neighbor and stranger stimuli ($F_{3,48} = 3.868$, $p = .007$).
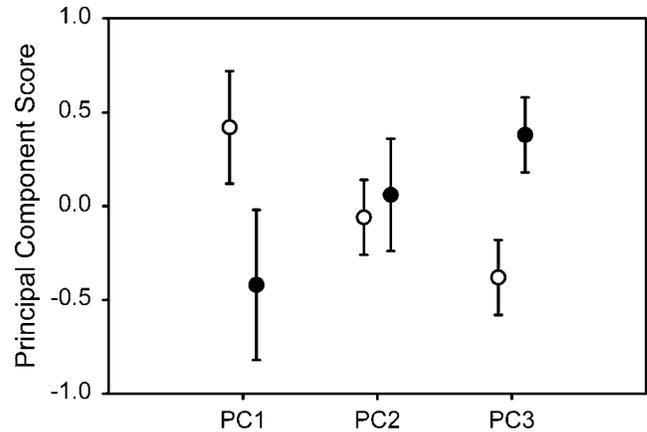
Figure 3
Mean scores (± SE) on the first three principal components for responses to neighbor songs (filled circles) and stranger songs (open circles) broadcast from the shared boundary of the subject.

Scores on the first and third PCs differed significantly between neighbor and stranger trials (one-tailed ANOVA on PC1: $F_{1,50} = 3.211$, $p = .03$; PC3: $F_{1,50} = 7.644$, $p = .004$) (Figure 3). There was no significant difference in PC2 scores (one-tailed ANOVA on PC2: $F_{1,50} = 0.086$; $p = .385$) (Figure 3).

DISCUSSION

Alder flycatchers demonstrate limited variation in songs within individuals, but had sufficient variation among individuals to permit statistical identification of songs of individuals in a population (Lovell and Lein, 2004). Despite the relatively restricted variation in their songs, alder flycatchers display the same type of NSD ability found in oscine species with much more variable songs. Our finding that they responded differentially to songs of strangers and songs of neighbors (Figure 3) led us to reject our null hypothesis that alder flycatchers would not discriminate between songs of neighbors and strangers.

We argue that the differential reaction to the two song stimuli indicates a more aggressive response to the songs of strangers. Subjects typically responded to songs of a stranger by flying toward the speaker more quickly, by 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 a neighbor. By approaching the speaker, an individual may signal a willingness to fight (Stoddard, 1996). Differences in the use of vocalizations in response to neighbor and stranger songs also support this conclusion. Alder flycatchers responded to songs of strangers primarily with aggressive call notes and to songs of neighbors primarily with fee-bee-o songs, a pattern that explains the apparent reversal of PC3 scores shown in Figure 3. Although some NSD studies have interpreted an elevated rate of singing as indicative of a "stronger" or "more aggressive" response, this is not necessarily the case (Stoddard, 1996). In natural territorial interactions between male alder flycatchers, singing essentially stops and birds vocalize almost exclusively with aggressive call notes during chases and close interactions. Only when they separate does singing resume. We argue that, 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.

As previously argued, alder flycatchers may benefit from NSD by conserving energy and avoiding injury resulting from fighting with neighboring individuals. With a reduction in the amount of time and energy spent responding to neighboring

individuals, territorial males can devote more time to attracting a mate or foraging.

The two previous studies of NSD in suboscines had design features that might weaken their conclusions. Although Westcott (1997) was concerned primarily with lekking behavior of the ochre-bellied flycatcher (*Mionectes oleagineus*), he found that males sang fewer songs in response to playback of songs of strangers than to songs of neighbors, indicating NSD. However, because he used a single stranger song as the stimulus in all playback trials, the possibility of pseudoreplication (the use of a sample size that is inappropriate to the hypothesis being tested) exists (McGregor et al., 1992). Westcott justified his use of a single stimulus song by noting that ochre-bellied flycatchers demonstrate no variation in song structure among individuals. However, there was no quantitative analysis to support this assumption. We have demonstrated that the songs of at least one suboscine vary consistently among individuals (Lovell and Lein, 2004). In contrast, Bard et al. (2002) found no difference in response to songs of neighbors and strangers in another Neotropical suboscine, the spotted antbird (*Hylophylax naevioides*), suggesting the absence of NSD. However, songs used as playback stimuli were not recorded during undisturbed singing, but were elicited from males by broadcasting conspecific songs. This could affect the nature or quality of the songs being recorded. If playback elicited song variants that were particularly aggressive, then the use of such songs as stimuli could mask differential responsiveness to neighbor and stranger songs.

Song learning has been suggested to be a "key adaptation" that has allowed oscines to undergo extensive radiation and to become the dominant group of birds (Baker and Cunningham, 1985). Raikow (1986) suggested that song learning might be correlated with high species diversity, making it a possible key adaptation, but dismissed the idea as incorrect and untestable.

The order Passeriformes is monophyletic (Ericson et al., 2003; Raikow, 1982). The two suborders are sister taxa, with the suboscines assuming the basal position within the clade (Ericson et al., 2003). The most parsimonious explanation is that song learning evolved after the oscines and suboscines diverged approximately 85–90 million years ago (Kroodsma, 1988). The question then arises as to why song learning would evolve in oscines and not in suboscines. Patterns of behavior and breeding ecology are similar in the two groups and, consequently, should generate similar selection pressures. Understanding how suboscines deal with the types of behavioral challenges that oscines meet using variation in their learned songs is critical to understanding the evolution and function of song in both suborders.

Our results challenge the "song learning equals oscine success" dogma and the designation of song learning as a key adaptation. Despite a mode of song development that does not involve learning, and the limited song variation that may be a consequence, alder flycatchers demonstrate the same type of discrimination and recognition abilities found in oscines, which learn their songs. The nature of song and its functions have gone virtually unstudied in suboscines. Our study is the first comprehensive test of NSD in a suboscine. Other than the two tests of NSD discussed previously, a study on song ranging in dusky antbirds (*Cercomacra tyrannina*; Morton and Derrickson, 1996) and three playback experiments investigating behavioral information provided by different vocalizations in three tyrannid flycatchers (Smith, 1988; Smith and Smith, 1992, 1996), work on suboscine song has been almost exclusively descriptive. Kroodsma (1996) suggested that the key to understanding the origins of vocal learning may lie with the suboscines. However, before we begin to answer that question, more research on song development, song function, and life histories of suboscines is necessary.

APPENDIX

Seventeen response measures recorded during song playback experiments testing neighbor-stranger discrimination of 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 |
| Number of wee-oo call notes |
| Latency to first wee-oo call note (s) |

REFERENCES

Bard SC, Hau M, Wikelski M, Wingfield JC, 2002. Vocal distinctiveness and response to conspecific playback in the spotted antbird, a Neotropical suboscine. Condor 104:387–394.

Baker MC, Cunningham MA, 1985. The biology of bird-song dialects. Behav Brain Sci 8:85–133.

Bee MA, Gerhardt HC, 2001. Neighbour-stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*), II: perceptual basis. Anim Behav 62:1141–1150.

Brindley EL, 1991. Response of European robins to playback of song: neighbour recognition and overlapping. Anim Behav 41:503–512.

Catchpole CK, Slater PJB, 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.

Ericson PGP, Irestedt M, Johansson US, 2003. Evolution, biogeography, and patterns of diversification in passerine birds. J Avian Biol 34:3–15.

Falls JB, 1982. Individual recognition by sounds in birds. In: Acoustic communication in birds, vol. 2 (Kroodsma DE, Miller EH, eds). New York: Academic Press; 237–278.

Falls JB, d'Agincourt LG, 1981. A comparison of neighbor-stranger discrimination in eastern and western meadowlarks. Can J Zool 59: 2380–2385.

Fisher J, 1958. Evolution and bird sociality. In: Evolution as a process, 2nd ed (Huxley J, Hardy AC, Ford EB, eds). London: George Allen and Unwin Ltd.; 71–83.

Gordon DM, 1989. Ants distinguish neighbors from strangers. Oecologia 81:198–200.

Kroodsma DE, 1982. Learning and the ontogeny of sound signals in birds. In: Acoustic communication in birds, vol. 2 (Kroodsma DE, Miller EH, eds). New York: Academic Press; 1–23.

Kroodsma DE, 1984. Songs of the alder flycatcher (*Empidonax alnorum*) and willow flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Kroodsma DE, 1988. Contrasting styles of song development and their consequences among passerine birds. In: Evolution and learning

(Bolles RC, Beecher MD, eds). Hillsdale, New Jersey: Lawerence Erlbaum; 157–184.

Kroodsma DE, 1989. Suggested experimental designs for song playbacks. Anim Behav 37:600–609.

Kroodsma DE, 1996. Ecology of passerine song development. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca, New York: Cornell University Press; 3–19.

Kroodsma DE, Konishi M, 1991. A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song with auditory feedback. Anim Behav 42:477–487.

Lambrechts MM, Dhondt AA, 1995. Individual voice discrimination in birds. Curr Ornithol 12:115–139.

Lovell SF, Lein MR, 2004. Song variation in a population of alder flycatchers. J Field Ornithol 75:146–151.

McGregor PK, 1992. Quantifying responses to playback: one, many, or composite multivariate measures? In: Playback and studies of animal communication (McGregor PK, ed). New York: Plenum Press; 79–96.

McGregor PK, Catchpole CK, Dabelsteen T, Falls JB, Fusani L, Gerhardt HC, Gilbert F, Horn AG, Klump GM, Kroodsma DE, Lambrechts MM, McComb KE, Nelson DA, Pepperberg IM, Ratcliffe L, Searcy WA, Weary DM, 1992. Design of playback experiments: the Thornbridge Hall NATO ARW census. In: Playback and studies of animal communication (McGregor PK, ed). New York: Plenum Press; 1–9.

McGregor PK, Westby GWM, 1992. Discrimination of individually characteristic electric organ discharges by a weakly electric fish. Anim Behav 43:977–986.

Molles LE, Vehrencamp SL, 2001. Neighbour recognition by resident males in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. Anim Behav 61:119–127.

Morton ES, Derrickson KC, 1996. Song ranging by the dusky antbird, *Cercomacra tyrannina*: ranging without song learning. Behav Ecol Sociobiol 39:195–201.

Ottoni EB, 2000. EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. Behav Res Methods Instrum Comput 32:446–449.

Raikow RJ, 1982. Monophyly of the passeriformes: test of a phylogenetic hypothesis. Auk 99:431–455.

Raikow RJ, 1986. Why are there so many kinds of passerine birds? Syst Zool 35:255–259.

Randall JA, 1994. Discrimination of footdrumming signatures by kangaroo rats, *Dipodomys spectabilis*. Anim Behav 47:45–54.

Reed JM, 1985. A comparison of the ''flush'' and spot-map methods for estimating the size of vesper sparrow territories. J Field Ornithol 56:131–137.

Rosell F, Bjørkøyli T, 2002. A test of the dear enemy phenomenon in the Eurasian beaver. Anim Behav 63:1073–1078.

Sibley CG, Monroe BL Jr, 1990. Distribution and taxonomy of birds of the world. New Haven, Connecticut: Yale University Press.

Smith WJ, 1988. Patterned daytime singing of the eastern wood-pewee, *Contopus virens*. Anim Behav 35:1111–1123.

Smith WJ, Smith AM, 1992. Behavioral information provided by two song forms of the eastern kingbird, *T. tyrannus*. Behaviour 120: 90–102.

Smith WJ, Smith AM, 1996. Playback interactions with great crested flycatchers, *Myiarchus crinitus* (Aves, Tyrannidae). Ethology 102: 724–735.

Stein RC, 1963. Isolating mechanisms between populations of traill's flycatcher. Proc Am Phil Soc 107:21–50.

Stoddard PK, 1996. Vocal recognition of neighbors by territorial passerines. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca, New York: Cornell University Press; 356–374.

Temeles EJ, 1994. The role of neighbours in territorial systems: when are they 'dear enemies'? Anim Behav 47:339–350.

Thomas ML, Parry LJ, Allan RA, Elgar MA, 1999. Geographic affinity, cuticular hydrocarbons and colony recognition in the Australian meat ant *Iridomyrmex purpureus*. Naturwissenschaften 86:87–92.

Westcott DA, 1997. Neighbours, strangers and male-male aggression as a determinant of lek size. Behav Ecol Sociobiol 40:235–242.

Whiting MJ, 1999. When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. Behav Ecol Sociobiol 46: 210–214.